EVALUATING THE ROLE OF EXOTIC DREISSENID MUSSELS IN THE DISAPPEARANCE OF THE BENTHIC AMPHIPOD *DIPOREIA* SPP. IN THE LAURENTIAN GREAT LAKES

A Dissertation

Presented to the Faculty of the Graduate School

of Cornell University

In Partial Fulfillment of the Requirements for the Degree of

Doctor of Philosophy

by

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May 2011

EVALUATING THE ROLE OF EXOTIC DREISSENID MUSSELS IN THE DISAPPEARANCE OF THE BENTHIC AMPHIPOD *DIPOREIA* SPP. IN THE LAURENTIAN GREAT LAKES

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Cornell University 2011

The burrowing amphipod *Diporeia* spp. has historically been the dominant macroinvertebrate and a high quality prey item for fish in benthic habitats of deep freshwater lakes of North America. In the mid-1990s, *Diporeia* populations began to decline in many of the Laurentian Great Lakes as exotic zebra and quagga mussels (*Dreissena* spp.) expanded after introduction from eastern Europe via transoceanic shipping. By 2010, this Great Lakes ecosystem health indicator had disappeared from vast areas of benthic habitat < 100 m depth in Lakes Erie, Ontario, Michigan, and Huron. Two common hypotheses for the decline of *Diporeia* are 1) dreissenids compete with the amphipod for food ("food limitation" hypothesis) or 2) dreissenids have carried some disease or toxin harmful to the amphipod ("pathogen" hypothesis). This study evaluated both hypotheses utilizing field and experimental approaches. The field component compared *Diporeia* 's response to dreissenid expansion in Lake Ontario to that in the Finger Lakes of central New York. *Diporeia* populations of Lake Ontario generally declined before quagga mussels expanded to depths >30 m, suggesting that remote ecosystem disruption by shallow mussels played a role. *Diporeia* populations in the Finger Lakes coexist with dreissenid mussels and represent a key anomaly to the pattern of decline seen in the Great Lakes. The experimental component of this study evaluated the pathogen and food limitation hypotheses by exposing *Diporeia* to dreissenids in controlled laboratory conditions.

Short-term (28-day) exposures using different combinations of *Diporeia* and quagga mussel populations did not indicate that quagga mussel populations from Great Lakes or Finger Lakes carry pathogens or toxins harmful to *Diporeia*. Longer-term (90-day) exposures suggest that the direct presence of dreissenids can actually benefit *Diporeia* leading to weight gain and higher fecundity relative to no-mussel controls. *Diporeia* may utilize biodeposits or periphyton associated with quagga mussels. A feeding trial with terrestrial organic matter (partially decomposed leaf litter), an alternative food source available in Cayuga Lake, also led to weight gain for *Diporeia* although survival was low. Fatty acid tracers, particularly the monounsaturate palmitoleic acid (16:1w7), were useful for assessing the dietary role of diatoms for *Diporeia*. The findings of my dissertation suggest that dreissenids may not have initiated the *Diporeia* decline. However, the continued expansion of dreissenid mussels in lakes Michigan, Huron, and Ontario is driving ecosystem disruptions including the disappearance of the spring diatom bloom that have major ramifications for the survival of remnant profundal populations of *Diporeia.*

BIOGRAPHICAL SKETCH

Many generations of Jim's family lived in the small dairy farming community of Cedar Grove, Maryland. He also grew up in Maryland in the suburbs of Washington, DC. He has always liked to hike and explore woods and streams and go fishing with his dad. He was an undergraduate at Cornell, majoring in geology but also taking many biology courses with an emphasis on paleontology. After graduation, he did internships studying the Chesapeake Bay, Bermuda, and the urban Anacostia River. These research experiences led him to enter a master's program in oceanography at Oregon State University, where he studied the current distribution of foraminifera, a plankton that has left an important fossil record, in the equatorial Pacific Ocean. Even though he enjoyed his trips to Hawaii and Tahiti, his next research project as a research technician was at an ice camp drifting north of Alaska for three months at a time. At least he got to stay on a ship rather than in a tent. He then joined the Sea Education Association as a shipboard oceanography instructor for six years. The group sails the Atlantic and Pacific Oceans with a pair of 130-foot schooners, teaching groups of 24 undergraduates how to sail and do scientific research. He came to the Cornell Biological Research Station in 2005 to work with Ed and Lars on a lower food web study of Lake Ontario.

ACKNOWLEDGEMENTS

The research within this dissertation was funded in part by the U.S. Environmental Protection Agency's Great Lakes Program Office of Chicago, IL (Grant # 00E36001-0 to Dr. Ed Mills). A small grant from Cornell's Biogeochemistry and Environmental Biocomplexity (BEB) program, a National Science Foundation funded Integrated Graduate Education and Research Training Grant (IGERT), funded the fatty acid analysis. New York State supported a 2007 study of the ecosystem of Owasco Lake that included our benthic surveys.

Undergraduate interns including Tom Stewart (Syracuse University), Mark Leopold (Cornell University), Dawn Moses (Cornell University) and Dana Seidel (Cornell University) provided invaluable help in the field and the laboratory.

My committee included Dr. Ed Mills, Dr. Lars Rudstam, Dr. Barbara Knuth, and Dr. Paul Bowser who guided me on my research approach and the writing process.

TABLE OF CONTENTS

LIST OF FIGURES

Chapter 1

Chapter 2

Chapter 3

LIST OF FIGURES

Chapter 4

LIST OF TABLES

INTRODUCTION

This dissertation evaluates potential mechanisms for the disappearance of the freshwater benthic amphipod *Diporeia hoyi* (formerly *Pontoporeia hoyi*) from large areas of the Laurentian Great Lakes. The lipid-rich crustacean has been present in sediments of deep lakes of North America for over ten million years (Väinölä and Varvio, 1989). Although small (2 to 10 mm), the amphipod historically occurred in great abundances (thousands of individuals per square meter) and often comprised up to 60% of the biomass in deep (>20 m) soft substrate benthic habitats (Sly and Christie 1992). *Diporeia* plays an important role in the coupling of pelagic and benthic ecosystems by consuming diatoms that sink to the sediment surface and returning this energy to fish as prey. In the mid-1990s, this species underwent dramatic population declines in the lower Great Lakes including Lakes Erie, Ontario, Michigan and Huron (Dermott and Kerec 1997, Dermott 2001, Nalepa et al. 1998, Nalepa et al. 2003). By 2006, *Diporeia* had disappeared from all but the deepest (>90 m) habitats in these four lakes (Nalepa et al. 2006a). This loss represents ecosystem disruption over 40-60% of benthic habitat of these lakes (>500,000 km^2), now largely colonized by the exotic quagga mussel *Dreissena rostriformis bugensis*.

Setting: The Great Lakes Basin

The Great Lakes Basin has a population of more than 30 million people and stores nearly 84% of surface water in North America and 21% of the world's supply of fresh water (US EPA and Government of Canada 1995). This extensive freshwater ecosystem provides several valuable ecosystem services including clean drinking water, water for agriculture and industry, waste treatment, transportation, food production, and recreation. Ecosystem services from lakes such as the Great Lakes

and rivers have been estimated to be worth $8498 1994 US dollars per hectare per year, much higher than that of temperate forests ($302 ha^{-1} yr^{-1}), grasslands ($232 ha^{-1} yr^{-1}), and croplands ($92 ha^{-1} yr^{-1}) (Costanza et al. 1997).

Human populations have impacted the Great Lakes ecosystem and its ability to continue to provide several vital ecosystem services. For example, several nearshore habitats show the long legacy of waste dumping. Industrial activities have contaminated sediments, water, and fish with heavy metals and organic toxins. Summer blooms of the nuisance algae *Cladophora* foul nearshore habitats (Hecky et al. 2004). Even far offshore, the phytoplankton base of the food web was disrupted from the input of excess phosphorus from surrounding watersheds in the 1950s-1960s (International Joint Commission 1969). At the top of the aquatic food web, several fish species have been driven to extirpation by intense fishing for food production (Christie 1972). Transportation, particularly commercial shipping (Ricciardi and MacIsaac 2000), has been the primary vector for several exotic aquatic plant and animal species that have overwhelmed native biotic communities and led to damage and control costs near 14 billion dollars (Pimentel 2005). Several exotic fish species have been intentionally introduced to create recreational sport fisheries with economic benefits but at an ecological cost including the displacement of native species (Ryder and Kerr 1984). U.S. and Canadian government agencies have acted in the form of environmental clean-ups, fishery regulations, and watershed phosphorus controls to tackle such problems as they arise. For example, eutrophication seen in the lower Great Lakes in the 1960s has been largely reversed (Millard et al. 2003) by the binational Great Lakes Water Quality Agreement (GLWQA) of 1972 that led to a ban of phosphorus based detergents, improvement of sewage treatment facilities, and the reduction of phosphorus in runoff from watersheds (International Joint Commission 1988).

Lake managers develop monitoring systems for detecting environmental change and a suite of 80 ecosystem indicators has been selected as particularly important to track the health of the Great Lakes Basin (Shear et al. 2003). Some indicators are chemical parameters that are useful in directly measuring the extent of pollution. Biological indicators are based on the status of specific organisms and may act as "canaries in a coal mine" in detecting ecosystem disruption. These species are selected for their broad spatial distribution and high connectivity to other organisms. A stressor responsible for a decrease in the abundance or condition of indicator organisms can therefore have ramifications throughout the food web. The subject of this dissertation, the benthic amphipod *Diporeia hoyi*, is the indicator selected by the State of the Lakes Ecosystem Committees (SOLEC) to represent the condition of the vast offshore component of the Great Lakes ecosystem (Neilson et al. 2003). A key ecosystem objective is to maintain a healthy, stable population of *Diporeia* in the profundal basins of the Great Lakes. Due to the current decline of *Diporeia* in many of the Great Lakes, SOLEC has described the status of *Diporeia* populations as deteriorating.

Importance of *Diporeia*

The loss of *Diporeia* in the Great Lakes has had a direct impact on the maintenance of two primary ecosystem services - food production and recreation. The many species of fish that depended on *Diporeia* have been forced to change their diet. For example, lake whitefish (*Coregonus clupeaformis*) switched to the native opposum shrimp (*Mysis diluviana*), dreissenid mussels, and other benthic invertebrates when *Diporeia* were not available (Owens and Dittman, 2003, Pothoven and Madenjian, 2008). This switch in prey led to the decline in both the abundance and condition of lake whitefish, a trend endangering the recovery of this highly valued

commercial species in Lake Ontario from an earlier collapse in 1970 caused by overfishing (Hoyle et al. 1999, Hoyle, 2005). *Diporeia* is also the primary food for two other native coregonids including lake herring (*Coregonus artedi*) and bloater (*Coregonus hoyi*), objects of ongoing restoration of native fish communities in the lower Great Lakes. Populations of the small benthivore slimy sculpin (*Cottus cognatus*) were reduced by over 95% between 1990 and 1996 in southeastern Lake Ontario in response to the disappearance of *Diporeia* (Owens and Dittman, 2003). This dramatic decline impacted the key recreational fishery for native lake trout (*Salvelinus namaycush*), the top native predator of the ecosystem.

Impacts from the loss of *Diporeia* also extend to non-native fish species that now dominate the open waters of the Great Lakes. Fishery managers introduced Pacific chinook salmon (*Onchorhynchus tshawytscha*) to the Great Lakes in the 1980s and created a multi-million dollar recreational fishery. Chinook primarily feed on the exotic alewife (*Alosa pseudoharengus*) and rainbow smelt (*Osmerus mordax*), two forage species that eat *Diporeia*. The loss of *Diporeia* in lakes Michigan and Huron has led to a decrease in weight and energy density for alewife (Madenjian et al. 2006, Riley et al. 2008).

Disappearance of *Diporeia*

The decline of *Diporeia* populations that has occurred since the mid-1990s has been closely associated with the expansion of exotic dreissenid mussels in the lower Great Lakes. The disappearance of the amphipod was first observed at 20-30 m depth in eastern Lake Erie (Dermott and Kerec 1997), the Kingston Basin of eastern Lake Ontario (Dermott 2001), southern Lake Michigan (Nalepa et al. 1998), and Saginaw Bay of Lake Huron (Nalepa et al. 2003) soon after zebra mussels (*Dreissena*

polymorpha) and quagga mussels (*Dreissena rostriformis bugensis*) colonized these habitats in the early 1990s.

The amphipod was extirpated from the relatively shallow (49 m maximum) eastern basin of Lake Erie by the early 1990s (Dermott and Kerec 1997). In deeper Lake Ontario, a decline of *Diporeia* populations at intermediate depths (30-90 m) was evident by 1995 as zebra and quagga mussels continued to thrive in shallower habitats (Dermott and Geminiuc 2003). In 1997, quagga mussels began to colonize soft substrate habitats that had previously been dominated by *Diporeia* (Lozano et al. 2001, Watkins et al. 2007, Chapter 1). This pattern of *Diporeia* disappearance followed by quagga mussel colonization has been repeated in lakes Michigan and Huron (Nalepa et al. 2009). By 2006, *Diporeia* had disappeared from all but the deepest (>100 m) habitats in lakes Ontario, Michigan, and Huron (Nalepa et al. 2006a). *Diporeia* populations have remained stable in Lake Superior (Scharold et al. 2004, Auer et al. 2009), the only Great Lake where dreissenids have not established.

Despite the general association of the timing of the decline of *Diporeia* with the expansion of dreissenid mussels, a closer look raises two important exceptions to this trend. First, *Diporeia* populations at many sites in deep habitats of the Great Lakes often declined before being directly exposed to detectable populations of quagga mussels. From 1995 to 2005, *Diporeia* populations at intermediate depths (30-90 m) in lakes Ontario, Michigan, and Huron had declined by more than 90% despite very low levels of quagga mussels (average densities $<1000/m^2$) in this depth interval (Nalepa et al. 2009). The decline of deeper *Diporeia* was associated with the increase in mussels in shallow (0-30 m) habitats. If mussels in fact play a role in the decline, this observation suggests that mussel populations in shallow habitats are remotely affecting deeper amphipod populations (Watkins et al. 2007, Chapter 1). Second, *Diporeia* has coexisted with dreissenid mussels in the New York Finger Lakes (part of

the Lake Ontario drainage) since 1994 (Dermott et al. 2005a, Chapter 2). *Diporeia* populations in the Finger Lakes are genetically very similar to impacted populations in lakes Huron, Michigan and Ontario, although they are distinct from Lake Superior populations (Pilgrim et al. 2009). The apparent resilience of Finger Lake *Diporeia* populations suggests that mussel impacts on *Diporeia* can vary in different lake systems.

The overall research question of my dissertation is:

"Why are *Diporeia* populations declining in most Great Lakes (lakes Erie, Ontario, Michigan and Huron) but not declining in Lake Superior and the New York Finger Lakes?

Diporeia populations in the Great Lakes have been studied for more than a century (Smith 1874). Although there are no historical events that compare with the current decline, population fluctuations of *Diporeia* have been commonly observed and attributed to a wide range of bottom-up and top-down acting mechanisms.

Pre-dreissenid mechanisms

Past fluctuations of *Diporeia* populations have been attributed to several factors including food supply, predation, and toxins. *Diporeia* consumes phytoplankton, particularly diatoms, that sink to the sediment surface. *Diporeia* populations have been estimated to consume up to 61% of the carbon deposited in the annual spring bloom in Lake Michigan (Fitzgerald and Gardner 1993). Diatoms are high quality food rich in polyunsaturated lipids that enhance growth and successful reproduction of aquatic invertebrates (Brett and Muller-Navarra 1997). After bloom

events *Diporeia* rapidly accumulates lipid stores important for survival during the rest of the year (Gardner et al. 1985). This cycle of feast and famine is repeated annually during the amphipods 2-3 year life cycle. For the closely related freshwater amphipod *Monoporeia affinis*, the abundance and growth of amphipod age classes were associated with the interannual variation of diatom flux in Sweden's Lake Vänern (Johnson and Wiederholm 1992). Consistent with the importance of food supply for growth and reproduction, the Great Lake with the lowest phosphorus and overall production, Lake Superior, historically had smaller *Diporeia* populations than the other more productive Great Lakes (Cook and Johnson 1974). Food limitation is a plausible cause for declines because of the dramatic decreases in the primary productivity that has occurred in the Great Lakes since the 1970s (Millard et al. 2003). Lower phosphorus levels have decreased phytoplankton biomass and led to shifts in the phytoplankton community. However, *Diporeia* abundance is currently higher in Lake Superior than in other Great Lakes even though primary production in Lake Superior is lower than in the other Great Lakes, a reversal of the historical trend (Auer et al. 2009). Therefore, declining productivity by itself does not completely explain the current decline of *Diporeia*.

Several fish species eat *Diporeia* and predation has been suggested as a force that structures *Diporeia* populations. For example, an observed twofold population decline in southeastern Lake Michigan from 1980 to 1985 was attributed to the resurgence of the native bloater after the stocking of Pacific salmon eased competition with alewife (McDonald et al. 1990). Sly and Christie (1992) concluded that *Diporeia* populations in Lake Ontario were less abundant than those of Lake Michigan due to more abundant sculpins. Evans et al. (1990) observed that sculpins of Lake Michigan selected large (> 8mm) *Diporeia* to the extent that few large *Diporeia* were found in sediments. Although convincing in these cases, sculpins are declining and their

predation pressure therefore does not explain the current decline of *Diporeia*. Additionally, none of these examples led to the complete disappearance of *Diporeia* observed in recent years.

Chemical contaminants have also been suggested as a stressor for *Diporeia*. For example, particularly low abundances of *Diporeia* in nearshore areas off the south shore of Lake Ontario in 1972 were attributed to polluted sediments near the Niagara River and the urban center of Rochester, New York (Nalepa and Thomas 1976). This hypothesis has been tested several times in laboratory settings. Bioassay studies have exposed live *Diporeia* to sediments from several sites in the Great Lakes (Gossiaux et al. 1993, Landrum et al. 2000, Dermott et al. 2005b). Exposure to sediments from highly degraded areas (e.g. Areas of Concern) did have an effect on survival. For example, sediments from a site in Saginaw River downstream of a wastewater treatment plant elevated mortality by 55% compared to control sediments for a 28-day test period (Gossiaux et al. 1993). Sediments from a nearshore site (Niagara Bar) in Lake Ontario also induced higher mortality (40%) in a similar study (Dermott et al. 2005b). However, these studies did not find significant increases of *Diporeia* mortality associated with sediments from typical offshore habitats including sites colonized by dreissenids. Therefore, sediment toxicity has not been considered to be a primary cause for the *Diporeia* decline.

Dreissenid-based Hypotheses

The association of the *Diporeia* decline with dreissenid mussel expansion is currently the focus of most research on this issue and the subject of this dissertation. Dreissenids are thought to impact *Diporeia* as a competitor for food resources ("competition" hypothesis) or as a vector for disease ("pathogen" hypothesis) (Nalepa et al. 2006a). The "competition" hypothesis suggests that filter-feeding dreissenids

intercept settling algal food before it reaches the sediment surface where it can be available to the burrowing amphipods. The "pathogen" hypothesis suggests that dreissenids carry a pathogen or produce a toxic substance that is harmful to *Diporeia*. As previously mentioned, not all observations support the dreissenid connection. First, deep *Diporeia* populations in the Great Lakes often declined before coming into direct contact with expanding quagga mussel populations. Therefore, if there is a dreissenid-related cause, then shallow mussel beds affect deeper *Diporeia* populations remotely, either by intercepting the sinking food supply or by releasing a toxin or pathogen that is carried by water. Second, *Diporeia* has coexisted with dreissenid mussels in the New York Finger Lakes (part of the Lake Ontario drainage) since 1994.

My exposure experiments (Chapter 3) and pathogen surveys by Messick et al. (2004) and Faisal (2008) could not confirm a role of pathogens in the decline of *Diporeia*. Therefore, the findings of my thesis instead favor the "competition" hypothesis. In the Great Lakes, mussel beds have intercepted a large portion of *Diporeia*'s algal food supply. This remote competition has been less harmful to *Diporeia* in the New York Finger Lakes because of the availability of an alternative food source (terrestrial organic matter) and generally higher productivity.

Organization of dissertation and research findings

Chapter 1, *Evidence for remote effects of dreissenid mussels on the amphipod Diporeia: analysis of Lake Ontario benthic surveys, 1972-2003*, was published in the Journal of Great Lakes Research in 2007 (Watkins et al. 2007). Based on several lake-wide benthic surveys, it documents the rapid decline of the *Diporeia* population of Lake Ontario from 1994 to 2003. During this time period, *Diporeia* abundance at intermediate depths (30-90 m) declined from levels > 5000/m^2 to < 100/m^2. *Diporeia* populations > 90 m also began to be impacted, declining from 2181/m^2 in 1999 to

545/m^2 in 2003. This decline began as zebra and quagga mussels (*Dreissena* spp.) became abundant in shallow habitats of Lake Ontario. Quagga mussels had nearly replaced zebra mussels by 1999. Quagga mussels were not abundant at depths > 30 m until 1997, and by 2003 were abundant at 100 m depth and were even collected at sites > 200 m. A recent survey in 2008 indicates that the decline of *Diporeia* and the expansion of quagga mussels have continued (Steven Lozano, Great Lakes Environmental Research Laboratory (GLERL), pers. comm.). The trend of quagga mussel expansion following *Diporeia* decline has been repeated in Lakes Michigan and Huron (Nalepa et al. 2009). An important observation from these time series from all three lakes is that the decline of *Diporeia* populations occurred before direct contact with dreissenid mussels. This suggests that shallow mussel beds have remotely affected deep *Diporeia* populations rather than via direct contact or competition.

Chapter 2, *Coexistence of benthic amphipod Diporeia and dreissenid mussels in the New York Finger Lakes*, contrasts the rapid decline of *Diporeia* in the Great Lakes discussed in the first chapter to their apparent resilience in the New York Finger Lakes. *Diporeia* was present in the six Finger Lakes investigated (Cayuga, Seneca, Skaneateles, Canandaigua, Keuka, and Owasco) from 2006-2010 despite the presence of dreissenid mussels since the 1990s (USGS Nuisance Aquatic Species (NAS) Database). The six lakes have different trophic states, maximum depth, and dreissenid mussel introduction history. For example, Skaneateles and Canandaigua Lakes are oligotrophic like the Great Lakes while Cayuga, Seneca, Keuka, and Owasco Lakes are more mesotrophic (Callinan 2001). Cayuga and Seneca are the deepest (>150 m), with Skaneateles and Canandaigua also deep (90 m) with a large cold hypolimnion. However, Keuka and Owasco Lakes are much shallower (50 m) and represent marginal habitat for *Diporeia*. Quagga mussels were established in Cayuga and

Seneca Lakes as early as 1994, but have only since 2008 established populations competing with zebra mussels in Keuka, Canandaigua, and Skaneateles Lakes. Quagga mussels have not expanded to Owasco Lake, which has only zebra mussels. I expected the lakes with the highest dreissenid abundances to have the lowest abundance of *Diporeia*. However, out of these three factors, trophic state emerged as the most important determinant of *Diporeia* abundance. *Diporeia* were most abundant (2000-3000/m^2) in mesotrophic Cayuga, Seneca, and Owasco Lakes. The lower abundance of *Diporeia* (1000/m^2) in Skaneateles and Canandaigua Lakes was consistent with the lower productivity of the two lakes. In contrast to my expectations, the two lakes with the most abundant dreissenids (Cayuga and Seneca Lakes) also had the highest abundance of *Diporeia*. In these two lakes, *Diporeia* often lives in direct contact with abundant (>1000/m^2) quagga mussels.

The coexistence of *Diporeia* and dreissenid mussels in the Finger Lakes provides questions and opportunities towards understanding the decline of *Diporeia* in the Great Lakes. First, the observation immediately puts into question the hypotheses that include a role of dreissenid mussels. Second, the anomaly leads to a series of hypotheses that can be tested in experiments involving populations of different lakes. Comparing *Diporeia*'s response to dreissenids in Great Lakes and Finger Lakes systems helps to separate dreissenid effects from other ecosystem differences.

Chapter 3, *Evaluating the role of pathogens in the disappearance of Diporeia in the Great Lakes*, outlines my experimental approach to investigating the possible dreissenid connection to the "pathogen" hypothesis for the decline of *Diporeia*. Dreissenid mussels harbor a microbial community that includes several known pathogens and varies considerably between water bodies (Winters 2008). If dreissenids are a vector for a pathogen or produce a toxin harmful to *Diporeia* in the Great Lakes, Finger Lakes mussels could simply be free of such pathogen or toxin. A

set of four testable hypotheses evaluated 1) transport of dreissenid-borne pathogens or toxins by water, 2) the effects of direct exposure to increasing levels of quagga mussels, 3) whether Great Lakes quagga mussels are more "toxic" to *Diporeia* than Finger Lake quagga mussels, and 4) whether *Diporeia* from Cayuga Lake and Lake Superior are more resistant to mussels than affected populations in the Great Lakes. Organisms for these experiments were collected during a survey of parasites and pathogens in *Diporeia* populations of the Great Lakes by Dr. Mohamed Faisal at Michigan State University (Faisal 2008). My experiments found no significant increase of *Diporeia* mortality due to exposure to quagga mussels over 28 days, no matter what populations of mussels or *Diporeia* were used. These findings suggest that the effects that dreissenids have on *Diporeia* populations may act over longer time scales than investigated, perhaps due to competition for food. Our findings were also consistent with the pathogen survey that found little evidence of disease in Great Lakes amphipod populations (Faisal 2008).

Chapter 4, *Utilization of alternative food sources by Diporeia in Cayuga Lake,* investigates the food limitation hypothesis. An experiment was conducted in microcosms over longer time scales (3 months) at which the effects of food limitation become more pronounced. Once a week, water in microcosms was replaced and sediments were stirred up, making organic carbon in sediments available to the quagga mussels. My hypothesis was that mussel interception would reduce the availability of organic matter to *Diporeia* over the long time period, and therefore *Diporeia* without quagga mussels would be larger and in better condition than treatments with quagga mussels. My findings contradicted this expectation- *Diporeia* living with quagga mussels grew larger and were in better condition after 3 months, suggesting that *Diporeia* can utilize dreissenid digestion products and periphyton on shells as sources of food. *Diporeia* also utilized decomposing leaf litter in feeding experiments and

maintained weight and lipid content. These findings confirm that *Diporeia* in Cayuga Lake can use alternative food sources to counter the interception of diatoms by dreissenids.

The findings of my thesis indicate that the expansion of dreissenid mussels may not be related to the disappearance of *Diporeia*. Field studies in the Great Lakes have found few examples of coexistence- amphipod populations disappear well in advance of mussel colonization. Exposing *Diporeia* to quagga mussels in controlled experiments fail to confirm any adverse effects from mussels from toxins, pathogens or competition for food. *Diporeia* actually appears to benefit nutritionally from direct contact and will actively seek out substrates with mussels in preference to substrate without mussels.

The findings of my thesis do not rule out that dreissenids have a remote impact on *Diporeia* populations. Competition for food between dreissenid mussels and *Diporeia* then occurs at the scale of the entire lake and depends on lake productivity and the availability of alternative food sources. The rapid expansion of zebra mussels in the early 1990s in shallow habitats of the Great Lakes brought the issue of invasive species to the public's attention. However, the replacement of zebra mussels by quagga mussels and its expansion to the deepest habitats of the Great Lakes has now become an even greater concern. Deep dwelling quagga mussels are capable of colonizing much more area of benthic habitat and therefore their filter feeding has a much greater impact on the overall lake ecosystem. Recent studies of Lake Michigan have identified a series of mussel-driven ecosystem disruptions including the disappearance of the spring diatom bloom and the collapse of zooplankton and fish communities (Vanderploeg et al. 2010). The decline of *Diporeia* populations, highly dependent on the spring diatom bloom, is a natural progression of this trend.

The findings of my thesis have several implications for ecosystem and fishery managers. First, *Diporeia* is likely to persist in Lake Superior despite the lake's low productivity. There is a low risk for dreissenid mussels to disrupt the lake ecosystem due to limiting calcium concentrations (Whittier et al. 2008). The *Diporeia* population of Lake Superior is genetically distinct from other Great Lakes populations (Pilgrim et al. 2009) and well adapted to low productivity lakes being "slimmer" (less weight per unit length), slower growing, and reproducing only once a year (Auer et al. 2009). Managers should continue to closely monitor *Diporeia* populations in Lake Superior but can likely count on the continued availability of this important prey item for benthivorous fish. Second, the persistence of *Diporeia* in the New York Finger Lakes, particularly Cayuga Lake, provides some degree of hope for the species since it remained resilient even after the establishment of dreissenid mussels in these lakes. Our observations in Cayuga Lake suggest that the availability of terrestrial organic matter is important as an alternative food source for *Diporeia*. Other key insights may emerge from the continued investigation into the differences in the impact of dreissenid mussels on the Great Lakes and the smaller Finger Lakes. Finally, managers must accept that *Diporeia* populations are unlikely to recover in lakes Michigan, Huron, and Ontario leaving opposum shrimp *Mysis diluviana* as an essential remaining prey item for fish populations. *Diporeia* has likely represented a "canary in a coal mine" whose disappearance foreshadows multiple levels of ecosystem disruption in the three lakes. Managers need to recognize the current fragility of these systems as they make key decisions including fish stocking levels.

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CHAPTER 1:

EVIDENCE FOR REMOTE EFFECTS OF DREISSENID MUSSELS ON THE AMPHIPOD *DIPOREIA* : ANALYSIS OF LAKE ONTARIO BENTHIC SURVEYS, 1972-2003*

*= A slightly modified version of this chapter appears as Watkins, J.M., Dermott, R., Lozano, S.J., Mills, E.L., Rudstam, L.G., and Scharold, J.V. 2007. Evidence for remote effects of dreissenid mussels on the amphipod *Diporeia*: analysis of Lake Ontario benthic surveys, 1972-2003. J. Great Lakes Res. 33: 642-657.

ABSTRACT

The status of invasive dreissenid mussels (*Dreissena polymorpha* and *D. rostriformis bugensis*) and native amphipods (*Diporeia* spp.) in Lake Ontario was assessed in 2003 and compared with historical data. *D. polymorpha* (zebra mussels) were rarely observed in 2003, having been displaced by *D. r. bugensis* (quagga mussels). *D. r. bugensis* expanded its depth range from 38 m depth in 1995 to 174 m in 2003 and this dreissenid reached densities averaging 8000/m^2 at all sites < 90 m. During the same time period, *Diporeia* populations almost completely disappeared from 0-90 m depth, continuing a declining trend from 1994-1997 reported in previous studies. The average density of *Diporeia* in the 30-90 m depth interval decreased from 1380/m^2 to 63/m^2 between 1997 and 2003. Prior to 2003, areas deeper than 90 m represented a refuge for *Diporeia*, but even these deep populations decreased, with densities declining from 2181/m^2 in 1999 to 545/m^2 in 2003. Two common hypotheses for the decline of *Diporeia* in the Great Lakes are food limitation and a toxin/pathogen associated with dreissenid pseudofeces. The *Diporeia* decline in deep waters preceded the expansion of quagga mussels to these depths, and suggests that shallow dreissenid populations remotely influence profundal habitats. This pattern of

decline is consistent with mechanisms that act from some distance including nearshore dreissenid grazing and downslope transport of pseudofeces.

INTRODUCTION

Historically, the benthic community of Lake Ontario was dominated by the amphipod *Diporeia* spp. which, together with fingernail clams (sphaeriids), oligochaetes, and chironomids, were the main components of the cold-stenothermal macrobenthic community occupying most of the deeper waters of all the Great Lakes (Cook and Johnson 1974). These organisms are primarily detritivores, dependant on surface production (particularly diatom blooms) sinking to the profundal areas (Gardner et al. 1989).

The 1990s was a decade of rapid transformation for the Lake Ontario benthic community. Two dreissenid mussel species *Dreissena polymorpha* (zebra mussels) and *D. rostriformis bugensis* (quagga mussels) were identified in 1989 and 1991, respectively (Griffiths et al. 1991, Mills et al. 1993). These non-native mussels are very efficient grazers of phytoplankton and may completely cover the lake bottom. Lake-wide studies documented the rapid spread of both species in shallow (0-30 m) habitats along the entire southern coast of Lake Ontario by 1995 (Lozano et al. 2001, Dermott and Geminiuc 2003). Between 1992 and 1995, an increase in the biomass of both species was observed, but the increase of *D. r. bugensis* was much greater and *D. r. bugensis* replaced *D. polymorpha* (Mills et al. 1999).

As dreissenids became firmly established at shallow depths, the abundance of the amphipod *Diporeia* decreased by 68% at intermediate depths (30-90 m) (Dermott and Geminiuc 2003, Lozano et al. 2001). Large annual fluctuations of *Diporeia* spp. and similar species in the family Pontoporeidae have been commonly observed in Lake Ontario (Dermott and Geminiuc 2003), the Baltic Sea (Andersin et al. 1978), and Swedish lakes (Johnson and Wiederholm 1989). These population fluctuations have been associated with food variability (Johnson and Wiederholm 1992) or intraspecific competition for food within or between year classes (Wenngren and Olafsson 2002).

In contrast, low abundances of *Diporeia* observed in nearshore waters of southern Lake Ontario during the 1970s were attributed to contaminants (Nalepa 1991). Increases of *Diporeia* abundance from 1970 to 1984 in northeast Lake Ontario have been attributed to lower predation pressure from slimy sculpin (*Cottus cognatus*) (Sly and Christie 1992), implying the converse, that an increase in fish predation could cause a *Diporeia* decline (McDonald et al. 1990). Dreissenid expansion and *Diporeia* decline during the 1990s have suggested possible competition between the two organisms for settling detrital food. Similar coupling between increases in dreissenid mussels and declines in *Diporeia* has been observed in Lake Michigan (Nalepa et al. 1998, Nalepa et al. 2006) and Lake Erie (Dermott and Kerec 1997), although Nalepa et al. (2006) could not establish a direct link between indicators of food availability and *Diporeia* declines in Lake Michigan. An alternative hypothesis for the decline focuses on the potential toxicity of dreissenid pseudofeces on *Diporeia*. Laboratory tests have shown a 25% decrease in survival of *Diporeia* exposed to pseudofeces for 90 days (Dermott et al. 2005).

Transformation of benthic communities in Lake Ontario has been detected by a series of lake-wide surveys. The earliest reliable surveys occurred in 1964-1966 (Hiltunen 1969, Barton and Anholt 1997). These studies documented the cold stenotherm character of the community and provided a baseline for abundance estimates. These surveys were followed by sampling programs such as the International Field Year for the Great Lakes in 1972 (IFYGL) (Nalepa and Thomas 1976), Canadian sampling in 1977 (Golini 1979), the Canadian Biomonitoring Program of the 1980's, the Canadian LOTT program in 1990 and 1995 (Dermott and Geminiuc 2003), and the US Environmental Protection Agency (US EPA) benthic community surveys in 1994 and 1997 (Lozano et al. 2001).

The objective of this study is to document continuing change of the Lake Ontario benthic community using lake-wide benthic surveys from 1998, 1999 and 2003. I discuss the likelihood of several mechanisms linking dreissenids to the decline of *Diporeia* given their observed spatial and temporal patterns in abundance. These include food reduction (grazing), chemical cycling (calcium uptake), and pathogen/toxin transport (pseudofeces). I also consider hypotheses exclusive of dreissenids that instead consider the role of lower lake productivity or fish predation.

MATERIALS AND METHODS

Sample Collection and Processing

The 1998 and 1999 data were collected using the stratified random design used in 1994 and 1997 (Lozano et al. 2001). 114 samples were collected on September 18-25, 1998 (Figure 1.1a) aboard the US EPA vessel R/V Lake Guardian and 67 samples were collected on August 22-28, 1999 (Figure 1.1b) aboard the R/V Lake Explorer. The benthic survey of 2003 consisted of five north-south transects of the binational Lake Ontario Lower Foodweb Assessment (LOLA) program (Figure 1.1c). These transects and site numbers are the same as surveys in 1990 and 1995 (Dermott and Geminiuc 2003). Grabs were collected at each of 37 sites over four separate cruises on August 10-11, August 18-20, September 21-25, and October 27, 2003 aboard the Canadian vessel CCGS Limnos and the R/V Lake Guardian.

Triplicate Ponar (area= 0.048 m^2 in 1998-1999, 0.053 m^2 in 2003) samples were pooled at each site. In 2003 only one grab was obtained at each of Sites 29 and 66. Mussels were removed prior to sieving to prevent damage to the concentrating net and placed in a labeled jar. Pooled triplicates were then placed in an elutriation device and washed through a nylon sleeve with a 500 μm mesh. Organisms were then

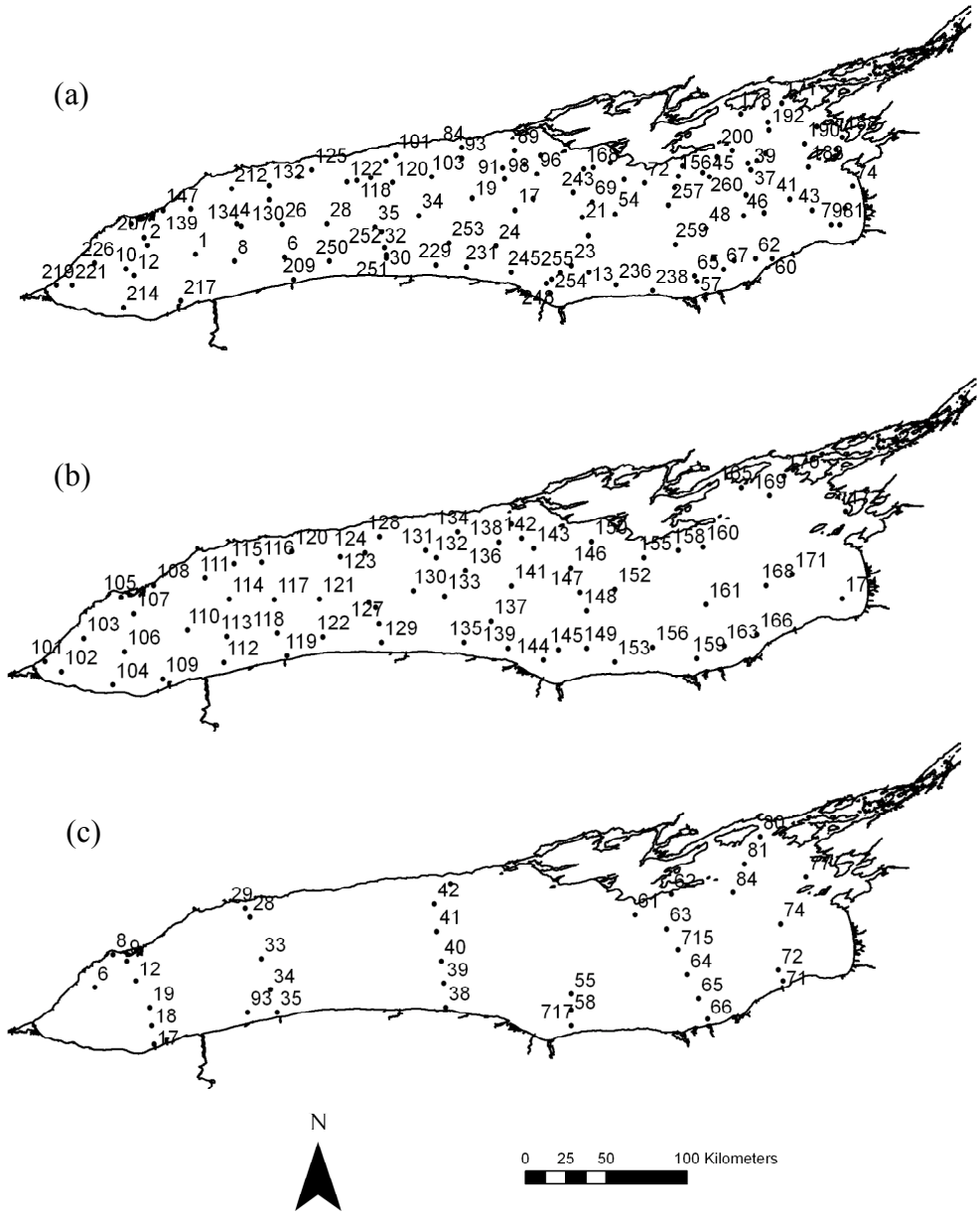


Figure 1.1. Maps of benthic survey sites sampled in 1998 (a), 1999 (b), and 2003 (c).

decanted into the jar with the mussels and preserved with 5-10% formaldehyde with a Rose Bengal stain. In 1998 and 1999, all organisms were identified. In 2003, only amphipods and dreissenid mussels were identified. Amphipods were identified as *Diporeia* spp., *Gammarus fasciatus*, and *Echinogammarus ischnus*, while mussels were identified as *Dreissena polymorpha* or *D. r. bugensis*.

Historical Data Sets

Results from 1998, 1999 and 2003 were compared to previous benthic surveys that also used Ponar grabs and 500-600 µm sieves. These data were collected in 1972 (Nalepa and Thomas 1976), 1990, 1995 (Dermott and Geminiuc 2003), 1994 and 1997 (Lozano et al. 2001). Dreissenids were not counted in the benthic survey in 1994.

Data Analysis

Distribution maps of *Diporeia, D. r. bugensis*, and *D. polymorpha* were made for 1990, 1994, 1995, 1997, 1998, 1999 and 2003 using Arc GIS (ESRI). Lake-wide averages for these and previous years were calculated by first separating samples into three categories by depth (0-30 m, 31-90 m, and >90 m). These depth intervals represent nearshore, slope, and profundal benthic habitats of Lake Ontario as defined in previous studies (Nalepa 1991, Lozano et al. 2001, and Dermott and Geminiuc 2003). Density data were logarithmically transformed ($\log_{10}$ (D+1)) before testing for significant differences. We tested for year and depth interval effects using a two-way ANOVA with both year and depth interval as categorical variables including the two-way interaction terms. Significant differences were then evaluated by post-hoc multiple range tests (Tukey's HSD). The abundances of oligochaetes and sphaeriids were also compared using a two-way ANOVA for 1972, 1990, 1994, 1995, 1997, 1998, and 1999.

RESULTS

Diporeia distribution and trends.

In 1998, 1999, and 2003, *Diporeia* were most abundant in the deep central basins of Lake Ontario (Figure 1.2). In 1998 and 1999, *Diporeia* abundance exceeded 1000/m^2 at several sites as shallow as 60 m in the Mississauga Basin and 100 m in the Rochester Basin. *Diporeia* were particularly abundant on the northern slope of the basins in comparison to the steeper southern slope. In 2003, *Diporeia* were rare at depths shallower than 90 m in the Mississauga Basin and 150 m in the Rochester Basin. *Diporeia* density exceeded 1000/m^2 at only one site in the deepest part of the Mississauga Basin (Site 40, 182 m) in that year (Table 1.1). In all three years, *Diporeia* were rarely found in shallow water along the northern and southern coasts and the Kingston Basin.

We compared our observations of *Diporeia* abundance to previous benthic surveys. From 1972 to 2003 (Table 1.2), significant differences of *Diporeia* abundance occurred for years ($F_{[7,458]}$=12.66, $P < 0.0001$), depth intervals ($F_{[2,458]}$=94.81, $P < 0.0001$) and year x depth interval interaction ($F_{[14,458]}$=6.12, $P < 0.0001$). Densities in the four recent surveys (1997, 1998, 1999 and 2003) were significantly less than in the four earlier surveys (1972, 1990, 1994, 1995) ($P < 0.05$, Tukey's HSD). Overall, sites > 90 m had significantly greater abundance of *Diporeia* than 31-90 m sites and < 30 m sites ($P < 0.05$, Tukey's HSD). The significant interaction term was caused by a time trend in the decline of *Diporeia* with depth; shallow populations declined before deep populations.

In 2003, *Diporeia* only occurred in central basin habitats represented by the deepest (>90 m) depth interval (Figure 1.3). These deep *Diporeia* populations had declined since 1999 but were not significantly different than those reported in 1972

Figure 1.2. Distribution of *Diporeia* in Lake Ontario for the years 1990 (a), 1994 (b), 1995(c), 1997(d), 1998(e), 1999(f) and 2003(g). Size of dots corresponds to density (#/m^2).

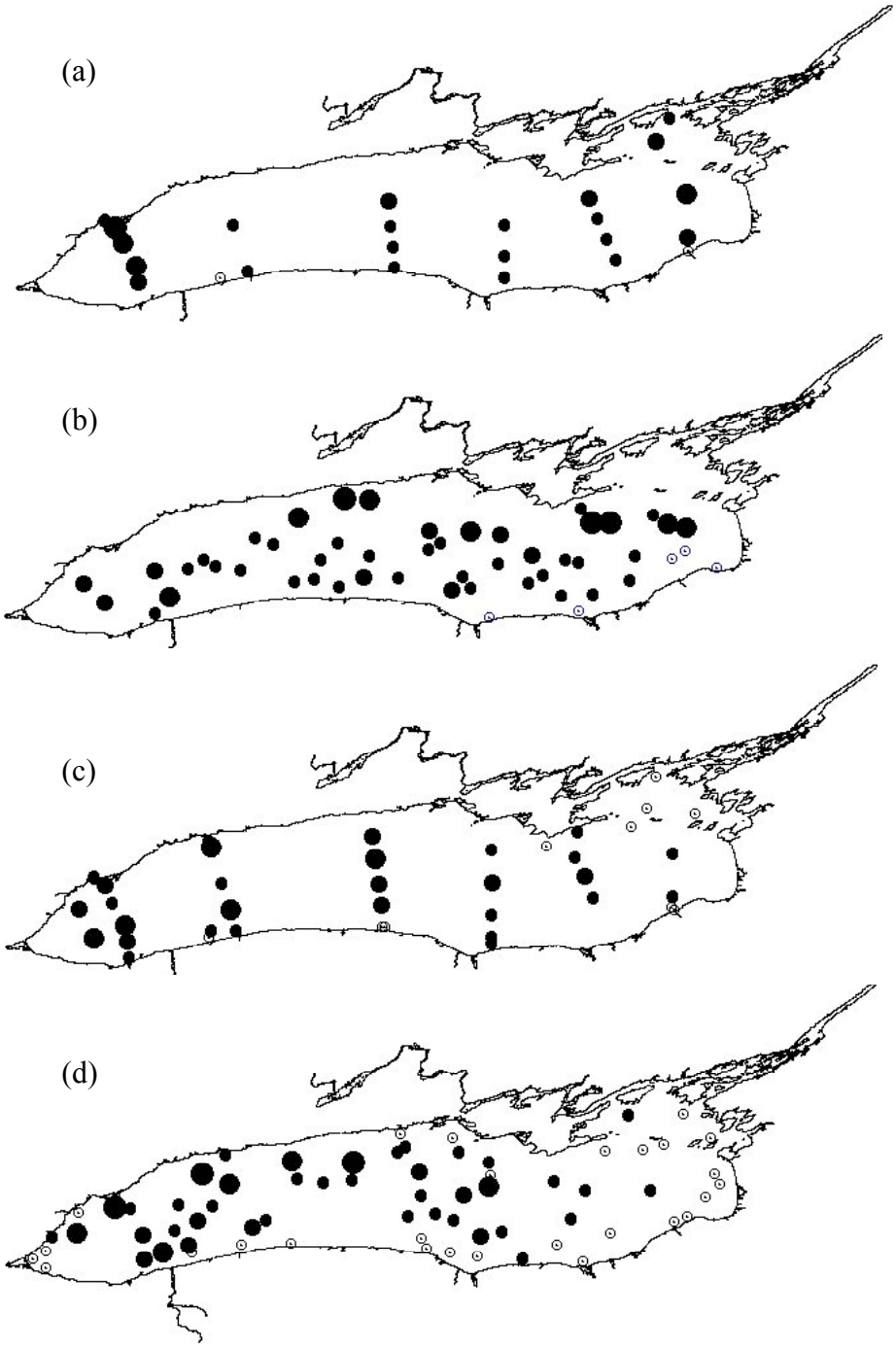

(a)
(b)
(c)
(d)

Figure 1.2 (continued)

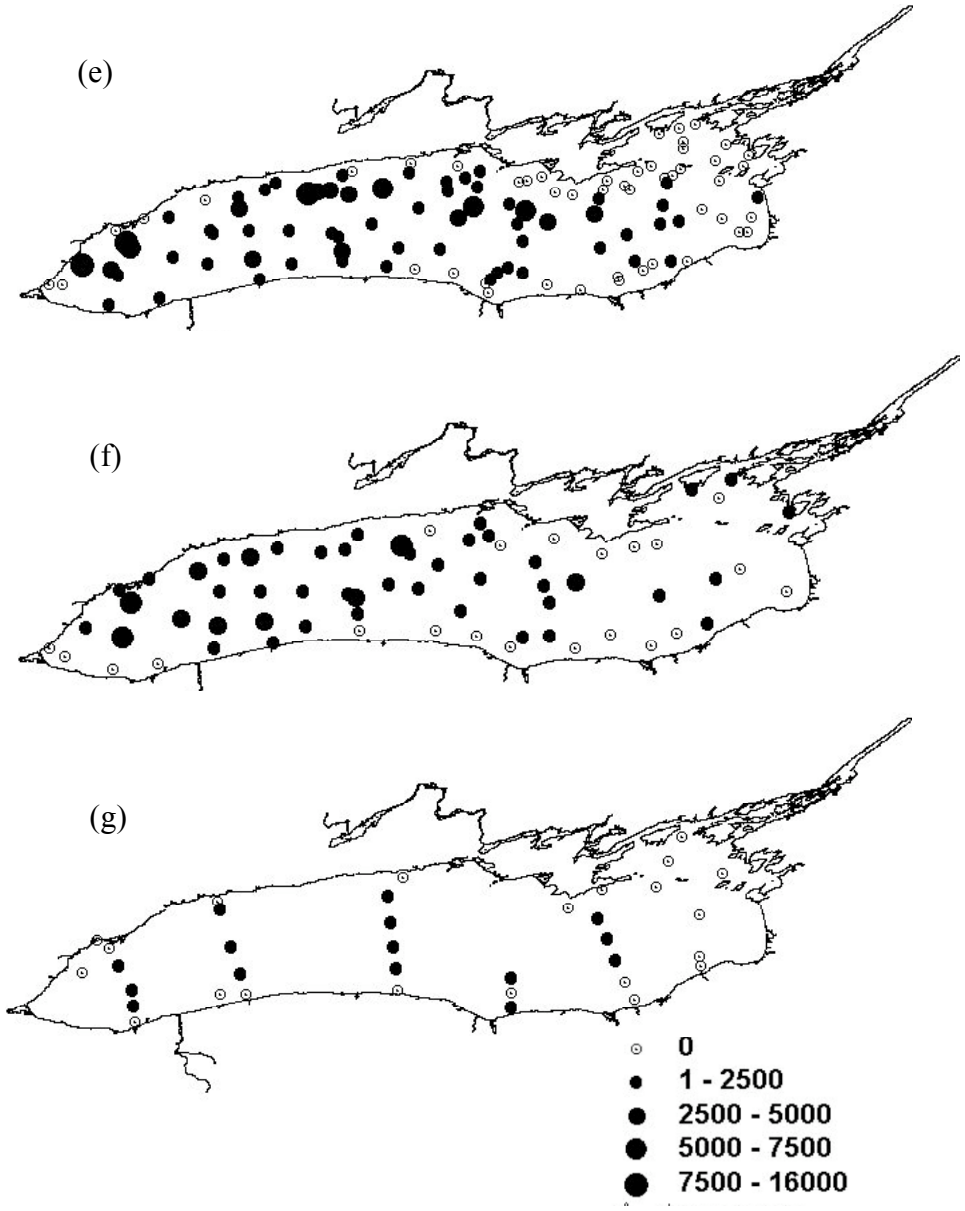


Table 1.1. Density (#/m^2) of *Diporeia* and *Dreissena* spp. in benthic surveys.

Site	Depth	*Diporeia*					*D. bugensis*					*D. polymorpha*				
	m	# m^{-2}					# m^{-2}					# m^{-2}				
		1990	1995	1998	1999	2003	1990	1995	1998	1999	2003	1990	1995	1998	1999	2003
0-30 m depth																
62	10	ns	19	0	ns	0	ns	0	342	ns	1600	ns	0	18	ns	0
17	11	ns	77	12	0	0	ns	39	262	955	2766	ns	19	0	162	397
8	15	19	0	0	15	0	0	0	787	2424	7869	0	0	12	0	0
66	18	ns	ns	0	ns	0	ns	ns	9754	ns	11340	ns	ns	22564	ns	19
38	19	38	0	ns	ns	0	0	1007	ns	ns	2104	38	5343	ns	ns	0
80	22	95	0	0	51	0	0	155	4990	3703	1978	0	426	85	73	0
71B	27	ns	ns	0	ns	0	ns	ns	5874	ns	31034	ns	ns	3019	ns	6
77	28	ns	0	0	ns	0	ns	155	1083	ns	20412	ns	136	555	ns	0
29	30	ns	19	ns	ns	0	ns	97	ns	ns	3213	ns	0	ns	ns	0
30-90 m depth																
81	35	3572	0	0	0	0	0	0	31	2571	6357	0	0	0	0	0
84	35	ns	0	0	ns	0	ns	39	98	ns	30045	ns	116	134	ns	0
35	37	19	116	6	15	0	0	10784	824	2219	2980	0	349	18	184	0
717	38	ns	39	0	0	6	ns	1142	378	7876	13564	ns	3427	49	0	0
43A	38	ns	ns	0	44	0	ns	ns	7649	4709	1802	ns	ns	0	0	0
61	53	ns	0	0	0	0	ns	0	927	793	4007	ns	0	6	0	0
9	60	10263	4588	ns	ns	0	0	0	ns	ns	504	0	0	ns	ns	6
28	61	ns	6815	908	1506	82	ns	39	18	1638	18440	ns	0	0	0	0
42	66	ns	3756	7027	5172	6	ns	0	0	544	13986	ns	0	0	0	0
74	68	6426	2304	ns	ns	0	0	0	ns	ns	6817	19	0	ns	ns	0
6	71	ns	4298	8393	2454	0	ns	0	6	0	4694	ns	0	0	0	0
93A	74	15806	1549	ns	ns	0	0	ns	ns	ns	6628	0	ns	ns	ns	0
18	87	2741	3194	ns	ns	781	0	0	ns	ns	25	0	0	ns	ns	0
63	87	4101	1897	48	ns	6	0	0	0	ns	3629	0	0	0	ns	0
>90 m depth																
58	99	2268	19	ns	176	0	0	0	ns	0	6904	0	0	ns	0	0
12	106	5368	2323	6301	7185	284	0	0	0	661	0	0	0	0	0	0
72	109	3818	19	0	ns	0	95	0	18	ns	3144	19	39	0	ns	0
19	109	5802	5092	2250	6663	473	0	0	0	0	0	0	0	0	0	0
41	129	3279	5673	2342	2263	945	0	0	6	0	6	0	0	0	0	0
33	137	491	2459	1665	1513	964	0	0	0	0	0	0	0	0	0	0
65	148	1909	ns	1262	0	0	0	ns	0	7	50	0	ns	0	0	0
715	151	775	2614	805	735	447	0	0	0	7	0	0	0	0	0	0
39	153	95	3156	1567	1381	479	0	0	0	0	0	0	0	0	0	0
34	174	ns	5750	3330	3188	636	ns	0	6	118	4114	ns	0	0	0	0
40	182	38	2614	2019	1168	1159	0	0	0	0	0	0	0	0	0	0
55	190	2136	1239	2196	1851	725	0	0	0	7	13	0	0	0	0	0
64	219	170	1529	622	360	977	0	0	0	0	50	0	0	0	0	0

Table 1.2. Average abundance(#/m^2) for deepwater benthic taxa (with s.e.) in Lake Ontario, 1972-2003.

0-30 m depth interval

Taxa	**1972**	**1990**	**1994**	**1995**	**1997**	**1998**	**1999**	**2003**
n	20	7	4	15	13	25	9	9
Diporeia	1728(609)	24(13)	46(46)	22(9)	22(21)	1(1)	202(138)	0
D. polymorpha	0	14(9)	nd	3108(1118)	1259(697)	2394(1259)	127(59)	47(44)
D. bugensis	0	0	nd	1798(1078)	774(390)	3472(1022)	1786(335)	9146(3428)
Sphaeriids	985(302)	1617(645)	129(45)	594(281)	244(92)	235(96)	375(150)	nd
Oligochaetes	8411(2930)	10760(3863)	3097(1484)	3854(1246)	1334(477)	1508(472)	2100(495)	nd

31-90 m depth interval

Taxa	**1972**	**1990**	**1994**	**1995**	**1997**	**1998**	**1999**	**2003**
n	15	6	12	15	27	49	30	14
Diporeia	2563(500)	5420(1356)	5167(769)	2328(615)	1380(449)	923(308)	613(226)	63(56)
D. polymorpha	0	3(3)	nd	11(8)	35(22)	10(4)	4(3)	0.4(0.4)
D. bugensis	0	0	nd	9(4)	590(267)	761(207)	4367(1131)	8106(2220)
Sphaeriids	208(89)	1024(422)	635(114)	1087(299)	388(141)	260(33)	216(35)	nd
Oligochaetes	5000(3005)	1693(763)	1227(265)	1702(436)	865(170)	610(113)	1178(282)	nd

> 90 m depth interval

Taxa	**1972**	**1990**	**1994**	**1995**	**1997**	**1998**	**1999**	**2003**
n	20	13	35	11	28	40	28	13
Diporeia	793(141)	2071(548)	1910(193)	3191(478)	1182(135)	2343(336)	2181(336)	545(111)
D. polymorpha	0	0	nd	0	0	0.2(0.2)	0	0
D. bugensis	0	7(7)	nd	0	0.5(0.3)	2(1)	35(24)	1100(614)
Sphaeriids	17(12)	235(114)	75(15)	83(28)	62(15)	108(17)	104(22)	nd
Oligochaetes	355(57)	522(162)	506(61)	671(159)	224(29)	274(49)	543(109)	nd

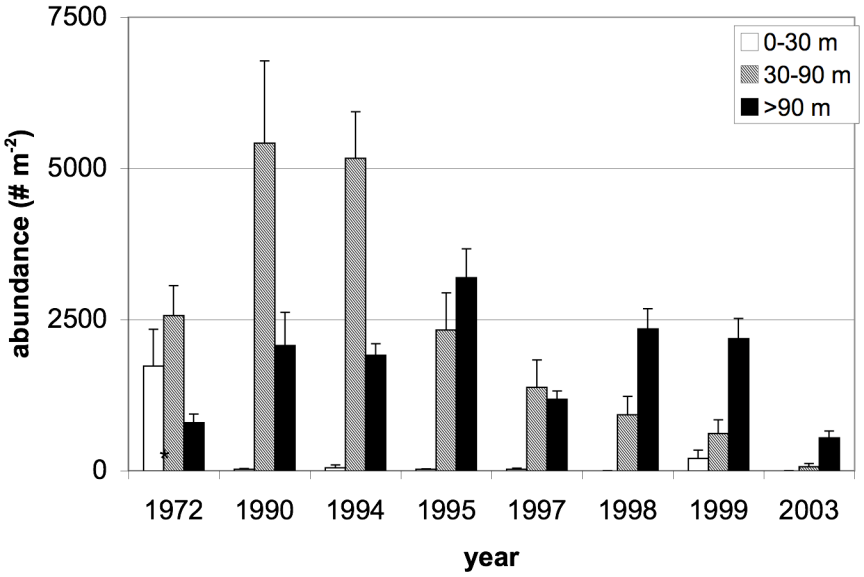


Figure 1.3. Average density (#/m^2) of *Diporeia* during 1972 through 2003 for three depth intervals: 0-30 m (shallow), 30-90 m (slope) and >90 m (profundal) regions. Error bars are one standard error.

($P < 0.05$, Tukey's HSD). *Diporeia* were nearly absent from the intermediate (30-90 m) depth interval in 2003, with a population averaging only 63/m^2 (95% decrease from 1997). The decline of *Diporeia* populations in this depth interval was first apparent from 1990 to 1995, a time period during which sharp decreases in abundance at five of seven specific sites contributed to an overall decrease of 60% (Dermott and Geminiuc 2003). Prior to the onset of this decline, *Diporeia* abundances in this depth interval had increased from 2563/m^2 in 1972 to > 5000/m^2 in 1990 and 1994. Shallow water *Diporeia* populations have been low since 1990 (Dermott and Geminiuc, 2003) with a slight recovery in 1999.

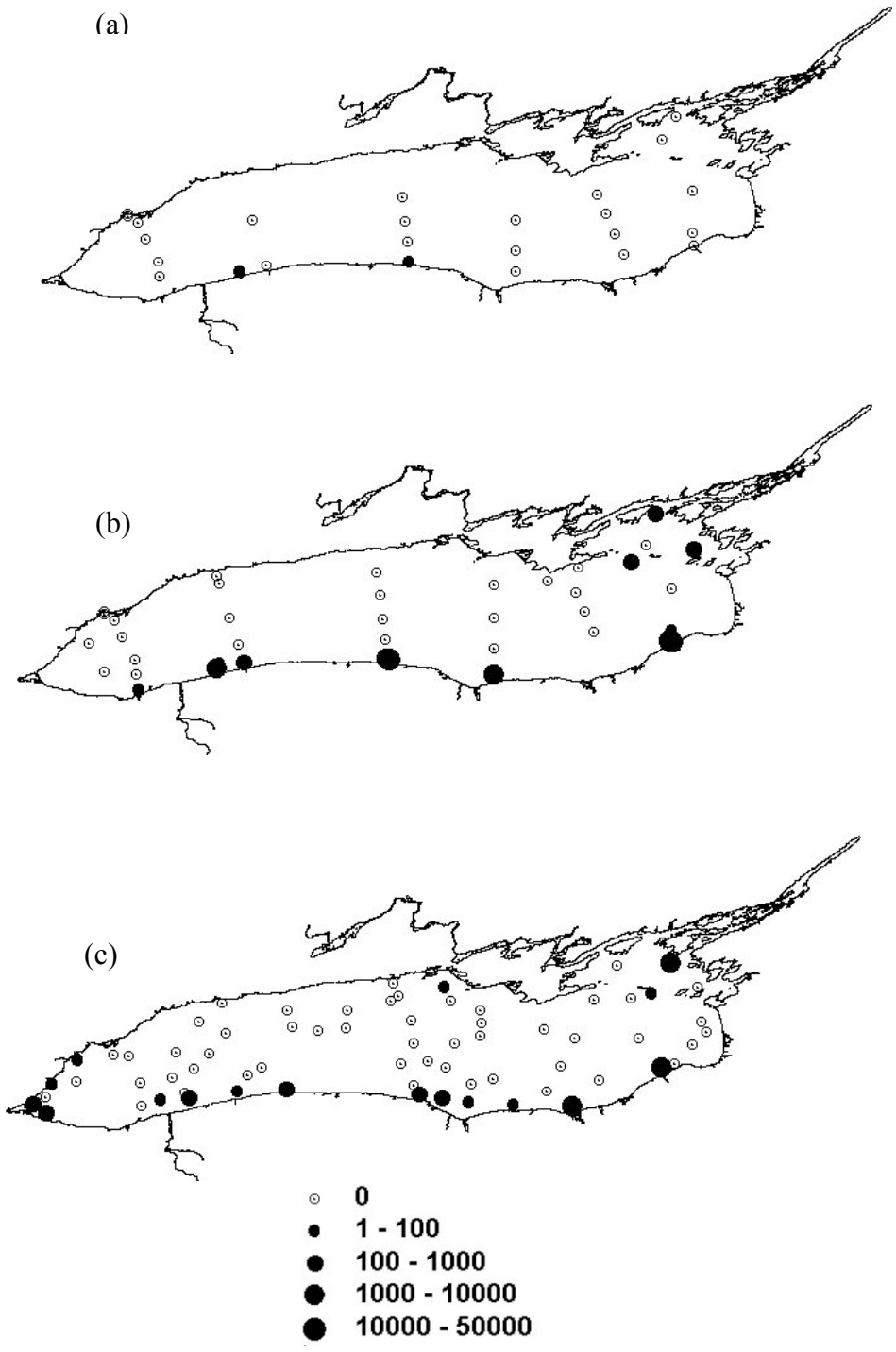
Dreissenid mussel distribution.

In 1998, *D. polymorpha* (zebra mussels) were abundant in shallow portions of the Kingston Basin and along both the southern and northern coasts (Figure 1.4d). In 1999, the species occurred only in the Kingston basin and near the Niagara River (Figure 1.4e). By 2003, the species was rare and only present at four nearshore sites, two in the east, and two in the west (Figure 1.4f). During all three years, zebra mussels were rarely collected from sites > 30 m.

The decline in *D. polymorpha* populations from 1999 to 2003 is significant when compared to previous surveys. From 1990 to 2003 (Table 1.2), significant differences of zebra mussel abundance occurred for years ($F_{[5,352]}$=5.61, P < 0.0001), depth intervals ($F_{[2,352]}$=68.47, P < 0.0001) and year x depth interval interaction ($F_{[10,352]}$=3.65, P = 0.0001). The abundances of the species from 1995-1999 were significantly greater than abundances in 1990 and 2003 (P < 0.05, Tukey's HSD). Abundances at shallow (0-30 m) sites were significantly greater than > 30 m sites (P < 0.05, Tukey's HSD).

In 1998, *D. r. bugensis* (quagga mussels) were abundant in shallow habitats throughout the lake, particularly on the north shore and the Kingston Basin (Figure 1.5d). By 1999, the species was more abundant in the 30-90 m depth interval than at shallow sites (Figure 1.5e. and Figure 1.6). In both years, quagga mussels were rare at sites > 90 m depth. By 2003, the species was abundant at nearly all sites < 90 m in depth, except Site 18 (87 m depth) on the western transect (Table 1.1). Quagga mussels also occurred at seven of 13 sites from > 90 m in depth. High abundances (>4000/m^2) of the species were observed as deep as 174 m (Site 34). However, quagga mussels were absent from at least one deep site on each transect.

Figure 1.4. Distribution of *D. polymorpha* (zebra mussels) in 1990(a), 1995(b), 1997(c), 1998(d), 1999(e), and 2003(f). Size of dots corresponds to density (#/m^2). Note logarithmic scale.


(a)
(b)
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0
1 - 100
100 - 1000
1000 - 10000
10000 - 50000

Figure 1.4 (continued)

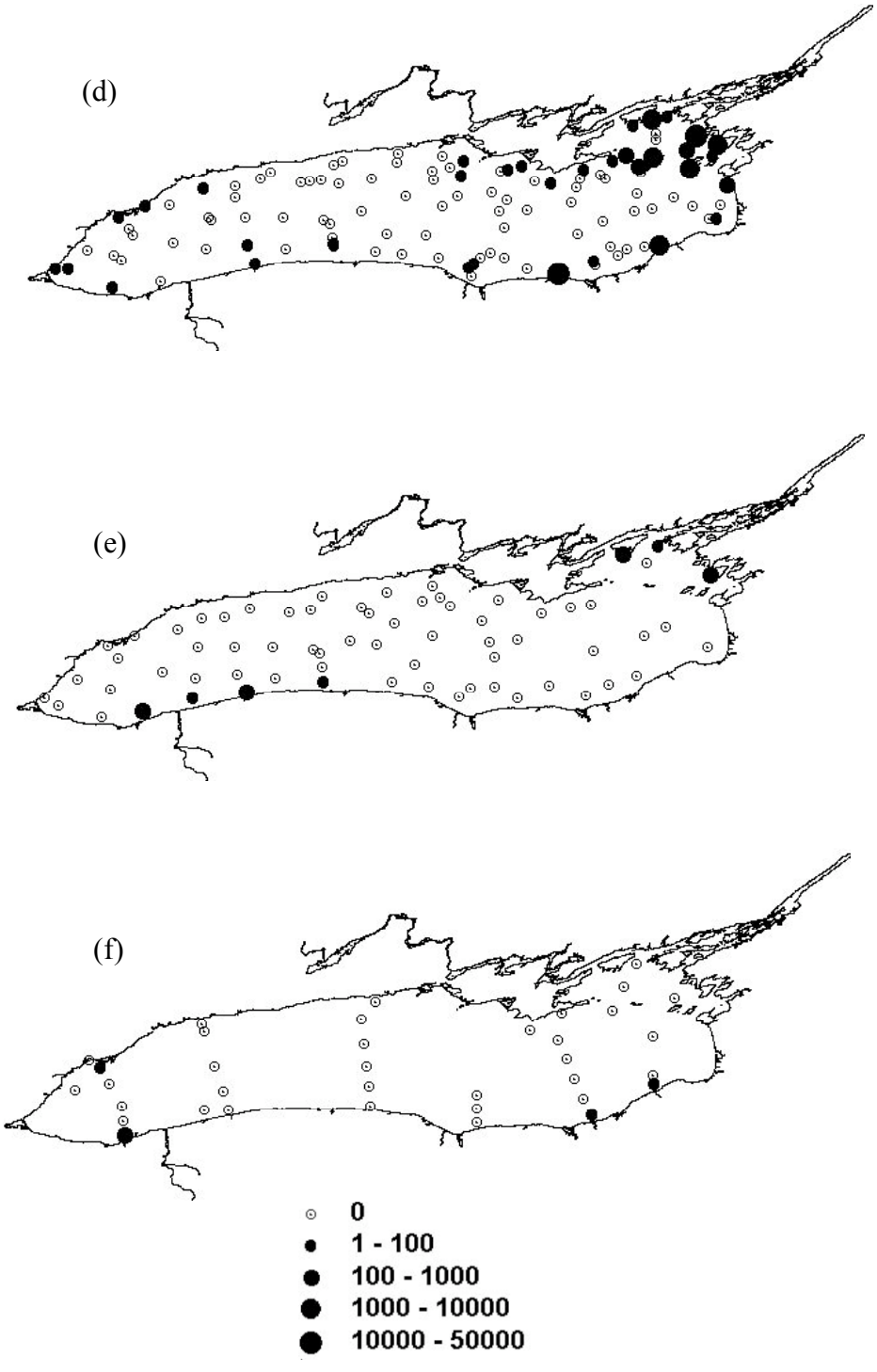


Figure 1.5. Distribution of *D. r. bugensis* (quagga mussels) in 1990 (a), 1995(b), 1997(c), 1998(d), 1999(e), and 2003(f). Size of dots corresponds to density (#/m^2). Note logarithmic scale.

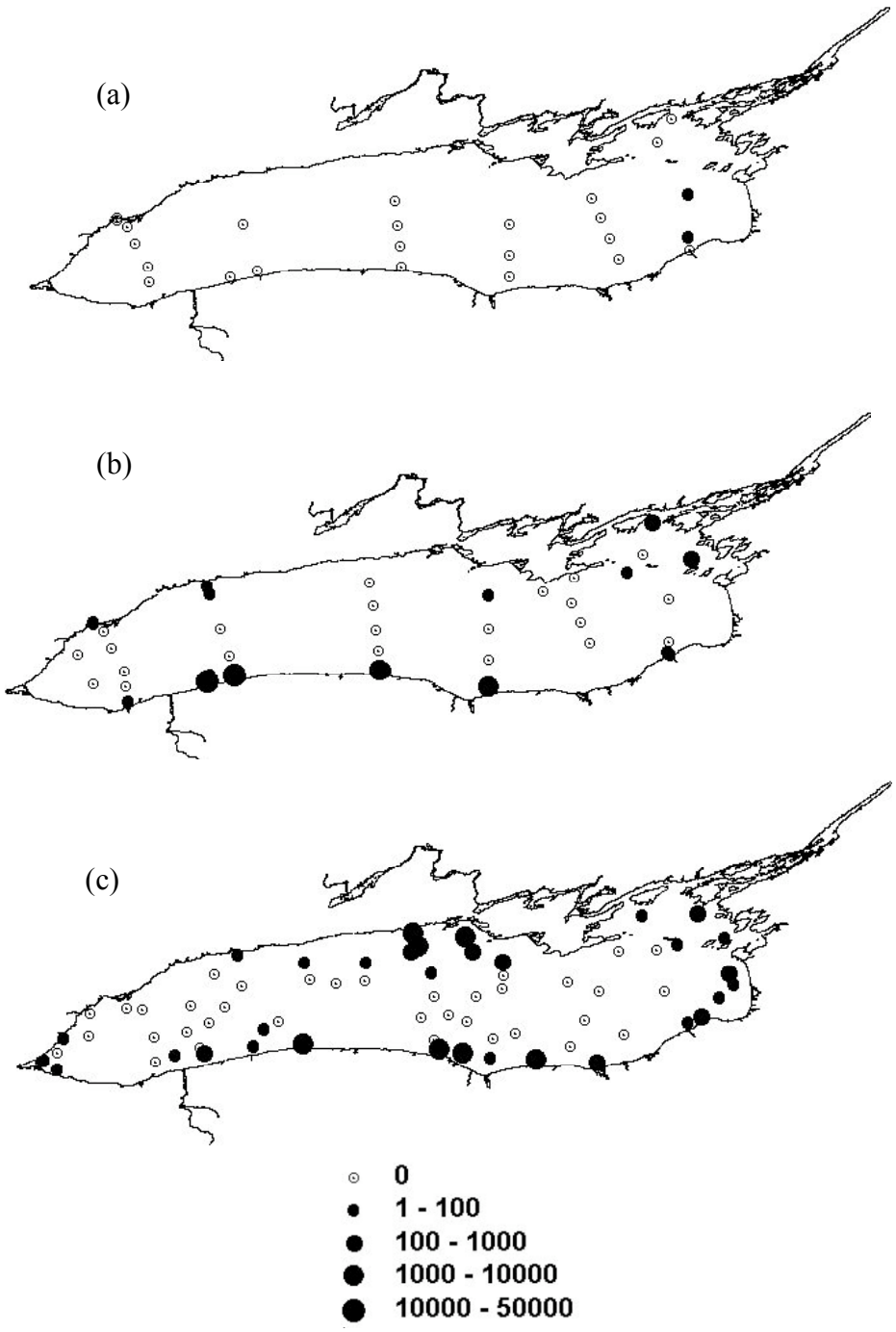
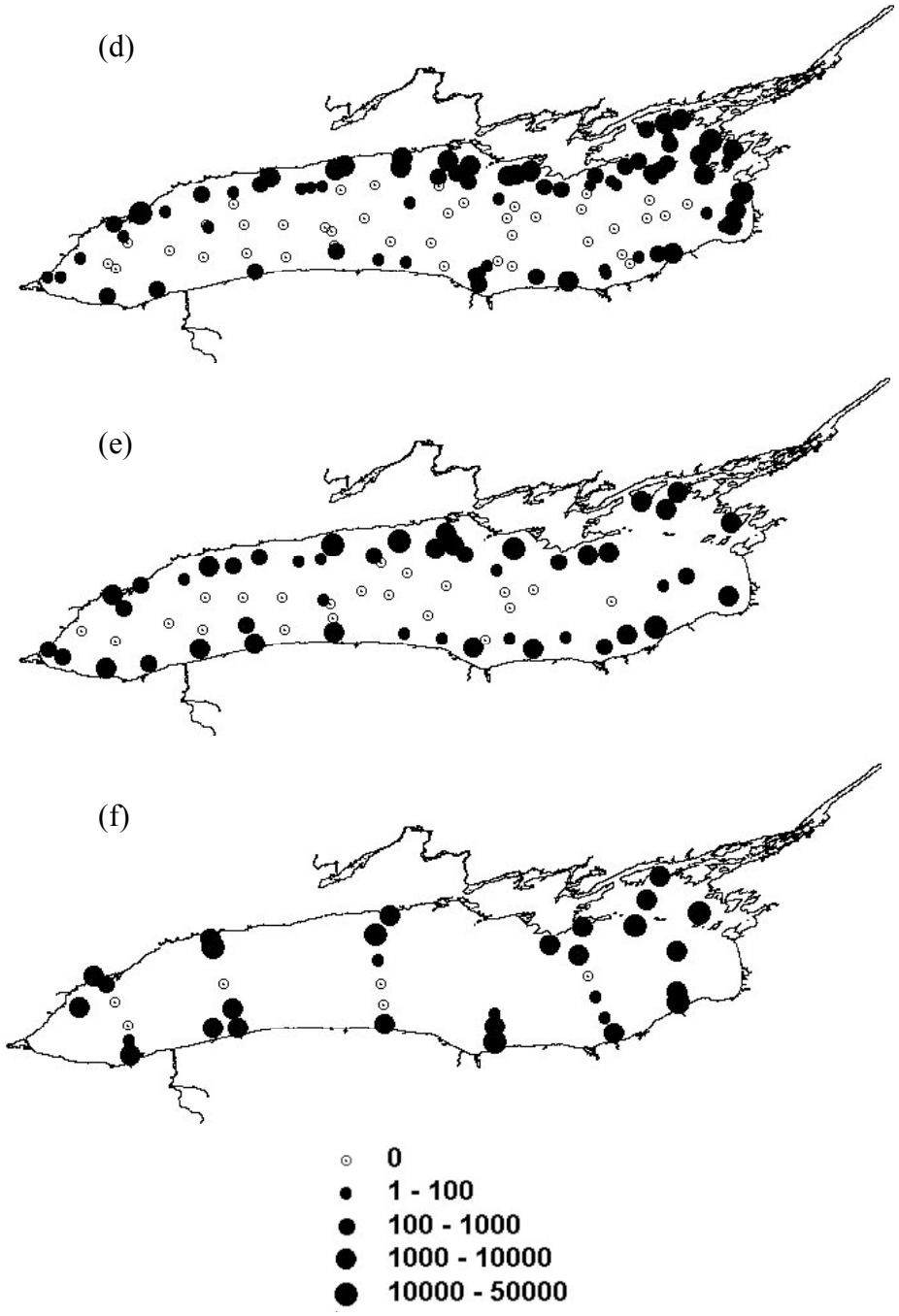

(a)
(b)
(c)
0
1 - 100
100 - 1000
1000 - 10000
10000 - 50000

Figure 1.5 (continued)



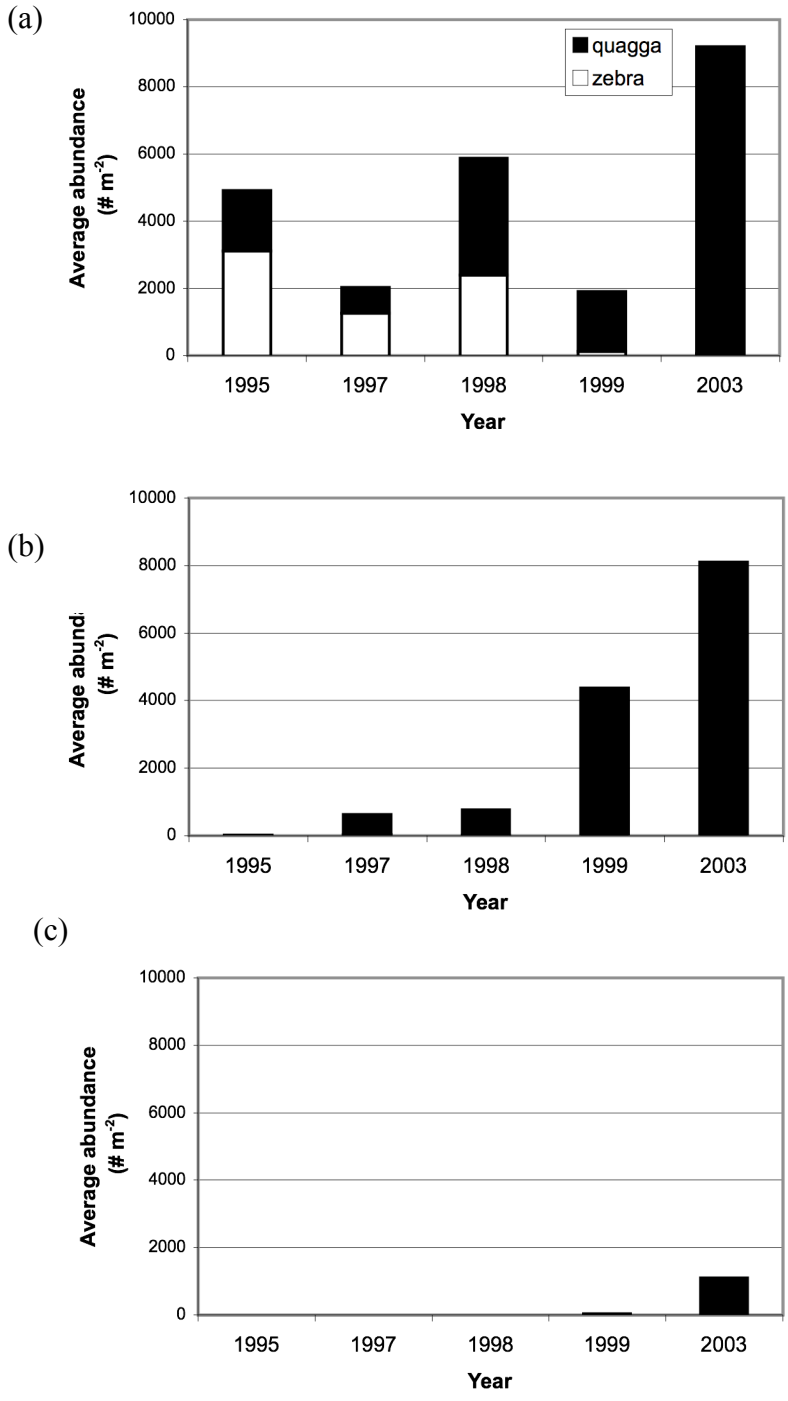


Figure 1.6. Change in dreissenid mussel abundance in the three depth intervals (0-30 m (a), 30-90 m (b) and >90 m (c) during the years 1995, 1997, 1998, 1999, and 2003. Note *D. polymorpha* (zebra mussels) and *D. r. bugensis* (quagga mussels) are denoted by white and black, respectively.

The expansion of *D. r. bugensis* is evident in the comparison with historical data sets. From 1990 to 2003 (Table 1.2), significant differences of *D. r. bugensis* abundance occurred for years ($F_{[5,352]}$=42.19, $P < 0.0001$), depth intervals ($F_{[2,352]}$=119.04, $P < 0.0001$) and year x depth interval interaction ($F_{[10,352]}$=8.43, $P < 0.0001$). The abundance of quagga mussels increased significantly each year from 1997 to 2003 ($P < 0.05$, Tukey's HSD). Abundances of the species were highest at shallow (0-30 m) sites, intermediate in the 30-90 m depth interval and lowest at the deep sites ($P < 0.05$, Tukey's HSD). The significant interaction term is due to the expansion of quagga mussels to deep habitats over time.

The historical data tracks the expansion of the two dreissenid species during the 1990s (Figures 1.4, 1.5 and 1.6). Both species were rare in 1990. By 1995, dreissenids were on the south shore and in the Kingston Basin, and abundance exceeded 1000/m^2 only at a few sites shallower than 38 m. By 1998, quagga mussels reached very high densities around the entire lake's nearshore and by 2003 had also extended into deeper water (Figure 1.5c-f, Figure 1.6). Increases in abundances of quagga mussels were evident at 18 of 20 sites < 90 m sampled in both 1995 and 2003 (Table 1.1). In contrast, the abundance of zebra mussels decreased between 1995 and 2003 (Figure 1.4c-f).

Sphaeriid and Oligochaete Distribution

From 1972 to 1999, significant differences of sphaeriid abundance occurred for years ($F_{[6,421]}$=5.97, $P < 0.0001$), depth intervals ($F_{[2,421]}$=31.36, $P < 0.0001$) and year x depth interval interaction ($F_{[12,421]}$=5.86, $P < 0.0001$) (Figure 1.7a). Densities in 1990 and 1995 were significantly greater (by 5 x) than abundances in 1972, 1997 and 1998 ($P < 0.05$, Tukey's HSD). Overall, intermediate sites 30-90 m had significantly greater abundance of sphaeriids than shallow and deep sites ($P < 0.05$, Tukey's HSD).

However, abundances at shallow sites were higher in 1972 and 1990 and contributed to the significant year x depth interaction.

Significant differences in oligochaete abundance were also apparent for years ($F_{[6,421]}$=12.82, P < 0.0001), depth intervals ($F_{[2,421]}$=37.39, P < 0.0001) and for year x depth interval interaction ($F_{[12,421]}$=2.44, P =0.045) (Figure 1.7b). Oligochaete abundances in 1997 and 1998 were significantly lower than abundances in all other years (P < 0.05, Tukey's HSD). Overall, shallow sites (0-30 m) had significantly higher abundances of oligochaetes than intermediate or deep sites (P < 0.05, Tukey's HSD). Shallow site abundances were three times the abundances at intermediate sites and six times the abundances at deep sites.

DISCUSSION

Status of the benthic community of Lake Ontario.

I consider the status of *Diporeia* in Lake Ontario in 2003 to be precarious. *Diporeia* was considered rare in shallow (0-30 m) habitats as early as 1990 (Dermott and Geminiuc 2003). More recently, however, *Diporeia* has experienced density declines in both intermediate (30-90 m, 1994 to 2003) and deep profundal (>90 m, 2003) regions of the lake. While the abundance of sphaeriids and oligochaetes significantly declined in the 12-88 m depth interval from 1994 to 1997 (Lozano et al. 2001), recent data (1999) suggests that the populations have stabilized for these taxa. We do not have enough data for these taxa to update their status for 2003.

The decline of *Diporeia*, sphaeriids, and oligochaetes coincided with the dramatic expansion of *D. r. bugensis*. The replacement of *D. polymorpha* by *D. r. bugensis* in Lake Ontario was first observed in 1995 (Mills et al. 1999), and was complete at depths < 30 m by 1998 or 1999. After quagga mussels replaced zebra

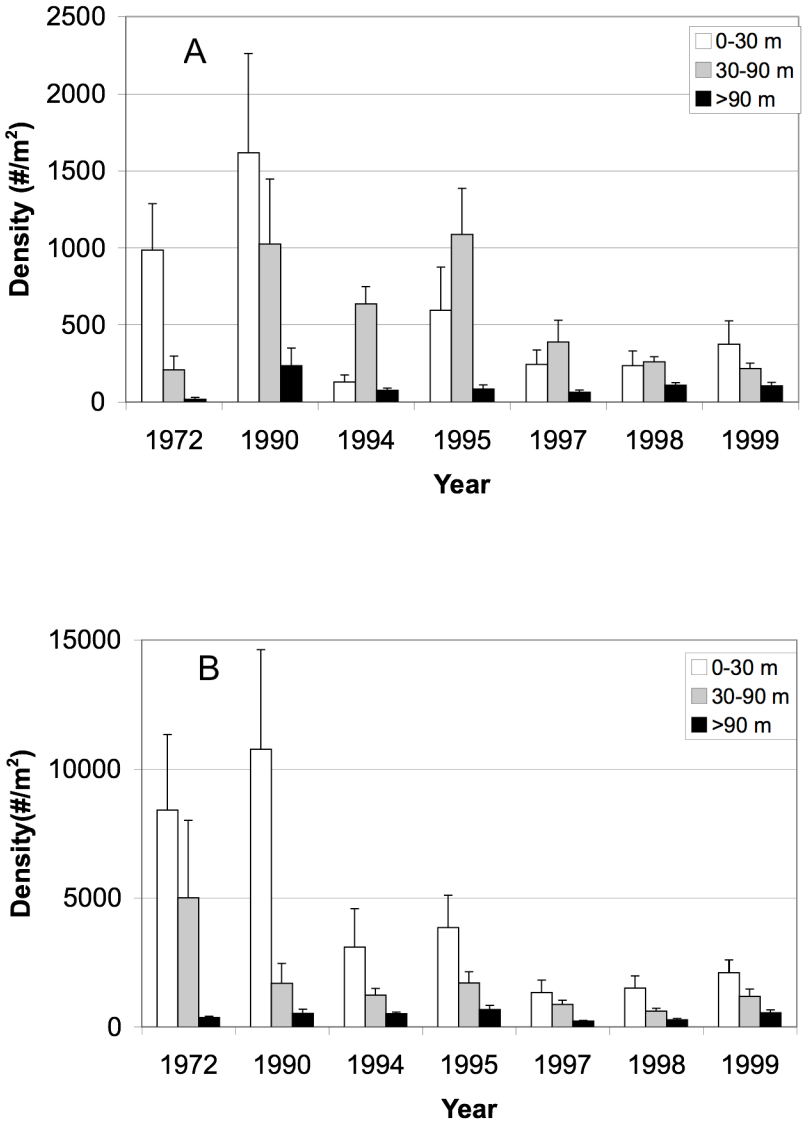


Figure 1.7. a) Sphaeriid and b) oligochaete abundance (#/m^2) for three depth intervals (0-30, 30-90 and >90 m) in the 1990's. Error bars are one standard error.

mussels in shallow habitats of Lake Ontario, quagga mussels expanded to deep habitats and were abundant in the 30-90 m depth interval by 1999. The expansion of quagga mussels into deep Lake Ontario habitats has no parallel within their native range (Mills et al. 1996). Recent studies, however, suggest that *D. r. bugensis* is better suited physiologically to handle cold temperatures than *D. polymorpha* (Baldwin et al. 2002, Stoeckmann 2003). By 2003, quagga mussels covered more shallow and deepwater habitat in Lake Ontario and attained higher densities than zebra mussels had in the early 1990's.

Comparison with other Great Lakes

The decline of *Diporeia* populations in Lake Ontario has also occurred in Lake Erie (Dermott and Kerec 1997) and Lake Michigan (Nalepa et al. 1998, 2006) in association with dreissenids. In the eastern basin of Lake Erie (30-64 m), *Diporeia* abundance declined 90% as *D. r. bugensis* became abundant from 1979 to 1993 (Dermott and Kerec 1997). In southern Lake Michigan, a decline in *Diporeia* abundance was first detected in 1992 at shallow (16-30 m) sites with *D. polymorpha* and had expanded to deeper sites (31-50 m) by 1993 (Nalepa et al. 1998). *Diporeia* populations steadily declined and *D. polymorpha* populations increased in Lake Michigan from 1993 to 2002. By 2002, *Diporeia* abundance had declined by 90% and *D. r. bugensis* was present at sites < 50 m (Nalepa et al. 2006). *Diporeia* populations are not declining in Lake Superior, the only Great Lake where dreissenids are absent (Scharold et al. 2004, Auer and Kahn 2004). These results suggest that dreissenids play a major role in the decline of *Diporeia* in the lower Great Lakes.

We can learn much about *Diporeia* from historical temporal and spatial studies of *Diporeia* and *Dreissena* in Lakes Michigan and Ontario. Two broad scale trends emerge from these studies: 1) the decline of *Diporeia* in these lakes first occurred in

shallow (<30 m) habitats soon after the introduction of *D. polymorpha*, and 2) a later decline of *Diporeia* populations occurred in intermediate (30-90 m) habitats in advance of the arrival of *D. r. bugensis* in this depth interval. We discuss potential mechanisms for the *Diporeia* decline given the observed spatial and temporal changes in abundance of both *Diporeia* and *Dreissena* in Lake Ontario through 2003.

"Food Limitation" hypothesis and lower lake productivity

Before considering the role of dreissenids, we need to first assess other potential mechanisms, including lower lake productivity and predation. Benthic production often reflects productivity in surface waters. The productivity of Lake Ontario has steadily decreased since 1975 in response to reductions in phosphorus loadings (Millard et al. 2003). Offshore spring total phosphorus (TP), an indicator of algal productivity in Lake Ontario, peaked at >25 μg/L in 1975, and declined to 10 μg/L by 1988 (Mills et al. 2003). This decline in TP was associated with a significant decrease in phytoplankton (chlorophyll *a*) and zooplankton biomass (Millard et al. 2003, Johannsson 2003). The reduced lake productivity could have significant impact on food resources for *Diporeia*. However, the historical data suggest that *Diporeia* increased at depths of >30 m between 1972 and 1990 even though TP and lake productivity declined. This population increase may be related to water quality improvements that also influenced nearshore benthic community composition from 1981 to 1991 (Kilgour et al. 2000). The later decline of *Diporeia* populations (1994 to 2003) in Lake Ontario occurred as offshore spring TP concentrations declined to 7 μg/L (Mills et al. 2006). In comparison, ultraoligotrophic Lake Superior has lower TP concentrations (2 μg/L TP) than Lake Ontario and *Diporeia* appear to be thriving. Lake Superior *Diporeia* populations in 2000 averaged 1300/m^2 in the U.S. nearshore waters of Lake Superior (Scharold et al. 2004), 300/m^2 on the shelf, 2266/m^2 on the

slope, and 524/m^2 in the profundal zone off the Keweenaw Peninsula (Auer and Kahn 2004). Current *Diporeia* populations in Lake Superior are less abundant than historical populations in other Great Lakes and may be limited by food supply. However, the presence of dense *Diporeia* populations in such a low productivity lake suggests that the disappearance of *Diporeia* from large areas of Lake Ontario is not a result of lower food supply. Evidence in Lake Michigan also discounts the role of lower lake productivity in the decline of *Diporeia* (Nalepa et al. 2006). In 1998, for example, *Diporeia* disappeared at site H-22 despite sufficient levels of organic flux and few dreissenids.

Survival of *Diporeia* in Lake Ontario may be linked to spring diatoms as lipid levels of the amphipod peak soon after the spring diatom bloom (Gardner et al. 1985). Dermott (2001) reported that declines of spring diatom biomass in the Kingston basin (0.6 g/m^3 to 0.1 g/m^3 in 1994 and 1995) coincided with the decline of *Diporeia*. Lake-wide diatom biomass in 2003 was at a historical low (Mills et al. 2006), and similar to that observed in 1995 (Mean of 0.13 g/m^3 in April and 0.02 g/m^3 in August (M. Munawar, unpublished data). Associated with decreased diatom production, silica concentrations in Lake Ontario have increased (Barbiero et al. 2002) but annual diatom productivity is not lower than that of Lake Superior. Since healthy populations of *Diporeia* currently exist in ultraoligotrophic lakes without dreissenids the *Diporeia* decline in Lake Ontario would not appear to be directly related to reduced phosphorus and flux of diatoms to the sediments.

"Predation" hypothesis

Fish predation could impact *Diporeia* populations as it is an important food for lake whitefish (Ihssen et al. 1981), slimy sculpin (*Cottus cognatus*), adult alewife, and rainbow smelt (Flint 1986). McDonald et al. (1990) suggested that an increase in

bloater (*Coregonus hoyi*) was the cause for a decline in shallow (<50 m) *Diporeia* populations in Lake Michigan from 1980 to 1984-85. Also, an increase in *Diporeia* in Lake Ontario from the 1970s to the 1980s has been attributed to a decrease in slimy sculpin (Barton and Anholt 1997, Sly and Christie 1992). However, the recent decline in *Diporeia* is not associated with an increase in their main piscine predators. In fact, both whitefish and slimy sculpins have declined (Hoyle et al. 2005, Owens and Dittman 2003), and adult alewife abundance has declined through the 1990s (O'Gorman et al. 2004) providing little support that fish predation has led to the decline of *Diporeia*.

Dreissenid effects: Local or remote?

Food limitation and pseudofeces toxicity are two mechanisms by which dreissenids could have contributed to the decline of *Diporeia* in the Great Lakes (Nalepa et al. 2005). An important issue is whether these mechanisms act locally or from some distance. Evidence supporting a remote influence is that the decline of *Diporeia* populations often occurred before dreissenids were detected in that same depth interval. For example, a sharp decline in the Lake Ontario *Diporeia* population in the 30-90 m depth interval (to 110 m in the southeastern part of the lake) occurred between 1990 and 1995 prior to the expansion of *D. r. bugensis* into that depth interval. Similarly, a 60-90 % decrease in *Diporeia* occurred between 1995 and 2003 at six deep sites where no quagga mussels were detected (Table 1.1). Thus, although we do not doubt that *Diporeia* and dreissenid mussels compete for the same food resources, we believe that it is unlikely that the decline was initiated by direct competition. That the decline in *Diporeia* preceded coexistence with quagga mussels suggests that the mechanism involved has to operate at a distance. Shallow (0-30 m) dreissenid populations impacted *Diporeia* populations living in the intermediate (30-

90 m) depth interval in 1995 and 1997. We believe the 2003 decline of *Diporeia* in the profundal (>90 m) region likewise was a response to the expanding quagga mussel populations in the intermediate (30-90 m) depth interval.

"Food Limitation" through dreissenid grazing

Intense phytoplankton grazing by zebra mussels in Lake Ontario (1990-1995) reduced chl *a* levels and increased water clarity, especially in shallow water habitats (Millard et al. 2003). After 1995, dreissenid populations in Lake Ontario expanded to deeper water habitats and shifted to a lower food tolerant dreissenid, *D. r. bugensis* (Baldwin et al. 2002). A similar dreissenid species shift has been observed for Ukrainian populations in Dneiper River reservoirs, where the two species are native (Mills et al. 1996). The expansion of quagga mussels to deep habitats has likely led to interception of particulate flux bound for deep benthos. There are two possible mechanisms for dreissenid grazing to affect *Diporeia* at a distance. First, nearshore regions are important for diatom production because of tributary contributions of silica, thermal bar structures, and upwelling events. Consequently, it is possible that dreissenid grazing in the nearshore region could intercept diatoms before they drift offshore and sink to profundal regions (Hecky et al. 2004). Second, the water column just above profundal sediments known as the benthic nepheloid layer (BNL) can be rich in organic matter (Urban et al. 2004). The BNL develops each summer in Lake Ontario during stratified conditions, and occurs at water depths greater than 60 m and extends 20-50 m above the lake bottom (Mudroch and Mudroch 1992). This organic matter originates from small epilimnetic phytoplankton and can be consumed by *D. r. bugensis*. It is possible that this rich source of organic matter is also food for *Diporeia*. If true, competition between *D. r. bugensis* and *Diporeia* for this important food source could be significant.

"Food Limitation" through dreissenid effect on lake-wide chemical cycling

Grazing is not the only mechanism by which dreissenids could influence benthic flux. Shell production by dreissenid mussels has dramatically reduced calcium and alkalinity levels in Lake Erie and Lake Ontario (Barbiero et al. 2006). Calcium concentration is a key factor in the precipitation of calcium carbonate in late summer, also known as "whiting" events (Strong and Eadie 1978). Lower calcium concentrations have been associated with increased offshore water clarity in the summer, an indication that whiting events have decreased. Whiting events also provide a major flux of organic matter (phytoplankton cells associated with calcite crystal formation) from the epilimnion to the sediment surface (Hodell and Schelske 1998), and a decrease in whiting events could therefore cause a reduction in food resources for *Diporeia*. However, inorganic carbon deposition rate measurements in Lake Ontario cores suggest that whiting events are recent phenomena, beginning in the 1940s with the onset of eutrophic conditions (Schelske et al. 1988). High phosphorus levels increased photosynthesis, which removed carbon dioxide and increased pH, causing calcite precipitation. As *Diporeia* were abundant in the Great Lakes before the 1940s, it is unlikely that this mechanism has contributed to the *Diporeia* decline.

"Pseudofeces and pathogens" hypothesis

Dreissenid waste (feces and pseudofeces) may be toxic to *Diporeia* or some pathogen associated with dreissenid mussels may be lethal (Nalepa et al. 2005, Dermott et al. 2005). Nearshore dreissenid beds produce large quantities of pseudofeces that may accumulate phytoplankton-derived toxins or carry biological pathogens. Decomposition of pseudofeces could lead to oxygen stress. Pseudofeces are very fine particles (<10 μm) that can be resuspended by currents and transported to offshore profundal areas (Lick et al. 1994). Dermott et al. (2005) found that the

addition of pseudofeces reduced *Diporeia* survival by 25% relative to controls in experimental tests. Dermott et al. (2005) also found that *Diporeia* was sensitive (75% less survival) to exposure to sediment where paralyzed and dying *Diporeia* had been placed for 48 hours and then removed. This observation suggests the influences of a pathogen, and both a microsporidian and a rickettsia-like parasite were found on some amphipods in this treatment. A pathogen could also spread to *Diporeia* from mussels even if the mussel density is very low, possibly low enough to not be detected.

CONCLUSIONS

It is clear that there is a strong negative association between *D. r. bugensis* and *Diporeia* in Lake Ontario and there has been no indication that *Diporeia* populations can recover after quagga mussels become established at a site, perhaps due to direct competition for food or space, or toxicity. This has led to a continuous displacement of *Diporeia* by *D. r. bugensis* in benthic habitats evident in 1990 for the 0-30 m depth interval, 1995 for the 30-90 m interval, and since 1998 for the >90 m depth interval (Figure 1.8). As quagga mussels continue to expand into the profundal regions, the population of *Diporeia* is expected to continue to decline. This pattern of decline with depth has been observed in all Great Lakes except for Lake Superior, where dreissenids have not been successful (Scharold et al. 2004). Therefore, we believe the decline in *Diporeia* is linked to the increase in *D. r. bugensis*, and mechanisms for the decline that do not involve dreissenids, such a decreased productivity and predation, are less likely.

However, the actual mechanism for causing the *Diporeia* decline is not known. Our observations that the decline of *Diporeia* precedes the appearance of *D. r. bugensis* in the same depth interval suggest that dreissenid populations can affect

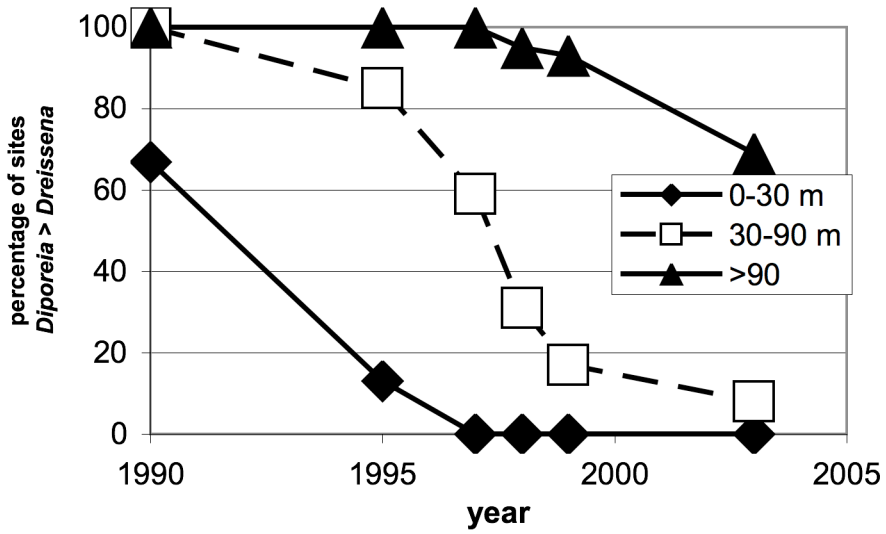


Figure 1.8. Percentage of sites where *Diporeia* outnumbered dreissenids in three depth intervals (0-30, 30-90 and >90 m) during lakewide surveys of Lake Ontario conducted from 1990 through 2003.

Diporeia from some distance or at least at very low dreissenid densities. We have identified two possible types of mechanisms. First, nearshore dreissenid grazing of phytoplankton may be diverting food resources from *Diporeia*. Dreissenid grazing of particles within deep nepheloid layers or the alteration of whiting event fluxes are less understood processes and would not affect the diatom fluxes most important to *Diporeia*. Second, toxic pseudofeces or a pathogen could be transported to deeper water by currents. A pathogen could also spread from rare, possibly undetectable early mussel colonists.

Whatever the cause, the loss of *Diporeia* has major implications for the capacity of the Lake Ontario ecosystem to support some native fish species. The amphipod represents a key link from phytoplankton production to fish. *Diporeia* are also relatively large and lipid-rich and therefore their loss is potentially more important than indicated by the decline in biomass alone.

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CHAPTER 2: COEXISTENCE OF THE NATIVE BENTHIC AMPHIPOD *DIPOREIA* SPP. AND EXOTIC DREISSENID MUSSELS IN THE NEW YORK FINGER LAKES

ABSTRACT

Populations of the benthic amphipod *Diporeia* spp. have sharply declined since the early 1990s in all North America's Great Lakes except Lake Superior. The onset and continued decline coincides with the invasion of these lakes by zebra (*Dreissena polymorpha*) and quagga (*Dreissena rostriformis bugensis*) mussels and particularly the spread of quagga mussels to deep habitats. The six deepest Finger Lakes of central New York (Seneca, Cayuga, Skaneateles, Canandaigua, Keuka, and Owasco) have historically been *Diporeia* habitat and now have had dreissenids for more than a decade. These lakes represent a wide range of trophic states, maximum depth, and dreissenid invasion history. If quagga mussel expansion is the cause of the continued decline of *Diporeia* in the Great Lakes, I hypothesized that *Diporeia* abundance would be negatively impacted by quagga mussel expansion in the Finger Lakes. During 2006-2010, I sampled *Diporeia* and mussel populations in the six lakes mentioned above. *Diporeia* was present in all six lakes, and was abundant (3000/m^2) in Owasco Lake that has only zebra mussels. However, *Diporeia* was similarly abundant in Cayuga and Seneca Lakes that have had quagga mussels since 1994. *Diporeia* abundance was lower (1000/m^2) in Skaneateles, Canandaigua, and Keuka Lakes where quagga mussels have recently expanded. Overall lake productivity is more important than mussel abundance in determining *Diporeia* abundance in the Finger Lakes. Fatty acid tracers indicate that *Diporeia* from Owasco Lake utilize diatoms more than *Diporeia* from Cayuga Lake which have food resources available from terrestrial detritus that cannot be intercepted by dreissenids.

INTRODUCTION

The benthic amphipod *Diporeia* (formerly known as *Pontoporeia*) has historically dominated soft substrate habitats of deep lakes of North America, often comprising more than 60% of total benthic biomass in deep (>20 m) habitats (Sly and Christie 1992). This burrowing amphipod feeds primarily on diatoms that sink to the sediment surface and it is a lipid-rich prey for many fish species including slimy sculpins (*Cottus cognatus*), lake whitefish (*Coregonus clupeaformis*) and deepwater coregonids (*C. hoyi and C. kiyi*). *Diporeia* therefore represents an important link between phytoplankton and fish production. During it's first meetings in 1994, the State of the Lakes Ecosystem Committees (SOLEC) recognized *Diporeia* as an indicator organism for assessing the condition of the offshore component of the Great Lakes ecosystem (Ryder and Edwards 1985, Neilson et al. 2003). Ironically, since selected as an indicator, *Diporeia* populations in many of the Great Lakes have been steadily deteriorating.

During the early 1990s, the disappearance of *Diporeia* was observed in shallow habitats in eastern Lake Erie (Dermott and Kerec 1997), eastern Lake Ontario (Dermott 2001), southern Lake Michigan (Nalepa et al. 1998), and Saginaw Bay of Lake Huron (Nalepa et al. 2003) soon after exotic zebra mussels (*Dreissena polymorpha*) and quagga mussels (*Dreissena rostriformis bugensis*) colonized these lakes. By the late 1990s, *Diporeia* at intermediate depths (30-90 m) in Lake Ontario were also in decline (Dermott and Geminiuc 2003, Lozano et al. 2001, Watkins et al. 2007). This pattern of *Diporeia* decline associated with quagga mussel expansion into deeper habitats has been repeated in Lake Michigan and Lake Huron, and *Diporeia* has disappeared from all but the deepest (>100 m) habitats in these lakes (Nalepa et al. 2009). *Diporeia* populations have remained stable in Lake Superior (Scharold et al. 2004, Auer et al. 2009), the only Great Lake where dreissenids have not been

successful probably due to low calcium concentrations. *Diporeia* populations have also persisted in many smaller lakes in Canada and the northeastern United States without dreissenid mussels (Dermott et al. 2005). Together this suggests a coupling between *Diporeia* decline and the invasion of the dreissenid mussels, possibly due to competition for the settling spring diatom bloom or dreissenids acting as a vector for some pathogen. Watkins et al. (2007, Chapter 1) and Nalepa et al. (2009) noted that *Diporeia* declined in deeper waters in both Lakes Ontario and Michigan before quagga mussels were abundant at these depths, indicating that shallower dreissenids may have played a role. Spring diatom blooms occur when the water column is well mixed, and quagga mussel biomass at intermediate depths in Lake Michigan has reached levels that can exert significant grazing pressure at that time (Vanderploeg et al. 2010). This observation provides a plausible mechanism for shallow mussel beds to intercept deeper *Diporeia*'s food supply.

One notable exception to the possible coupling between mussel increase and *Diporeia* decline is that *Diporeia* has reportedly persisted in two lakes, Cayuga and Seneca Lakes of central New York, as recently as 2001 despite the presence of dreissenid mussels for more than a decade (Dermott et al. 2005). There are six Finger Lakes (Seneca, Cayuga, Skaneateles, Canandaigua, Keuka, and Owasco) that are suitably deep (>50 m maximum depth) for *Diporeia* habitat and have year-round oxygenated cold hypolimnia (Table 2.1, Callinan 2001). Within a small geographic area, these lakes represent a broad range of trophic states ranging from oligotrophic Skaneateles Lake to mesotrophic Owasco Lake (Schaffner and Oglesby 1978). All six lakes have dissolved calcium levels > 28 mg/L and are therefore at "high risk" for invasion by dreissenid mussels (Callinan 2001, Whittier et al. 2008). Zebra mussels were reported in the lakes at different times, as early as 1991 in Cayuga Lake and as late as 1997 in Owasco Lake (USGS NAS Database, Table 2.1). Two of the lakes,

Table 2.1. Limnological characteristics of the six deepest Finger Lakes sampled in this study.

Lake	Maximum Depth(m)	Average Depth (m)	Surface Area(km2)	Avg 1996-1998 Values TP ug/L	chl a ug/L	Secchi m
Seneca	198.4	88.6	175.4	9.8	2.4	6.0
Cayuga	132.6	54.5	172.1	9.7	3.5	4.0
Skaneateles	90.5	43.5	35.9	4.0	0.7	7.6
Canandaigua	83.5	38.8	42.3	6.2	1.0	7.7
Keuka	55.8	30.5	47.0	8.0	2.8	5.6
Owasco	54.0	29.3	26.7	12.0	3.8	2.8

	Reported First Sighting USGS NAS Database	
	Zebra	Quagga
Seneca	1992	1994
Cayuga	1991	1994
Skaneateles	1995	2010
Canandaigua	1994	2010
Keuka	1994	2008
Owasco	1997	none

Cayuga and Seneca Lakes, have had quagga mussels since 1994. Quagga mussels were reported in Keuka Lake in 2008, indicating that quagga mussels have recently expanded to other Finger Lakes (USGS NAS Database). Therefore, the six lakes offer the opportunity to test several factors that regulate *Diporeia* abundance including trophic state, depth, and the abundance of the two dreissenid species.

In this paper I report on surveys (2006-2010) of the benthic invertebrates of the six deepwater Finger Lakes (Seneca, Cayuga, Skaneateles, Canandaigua, Keuka, and

Owasco Lakes). I expected to see a negative impact of dreissenid expansion on the abundance of *Diporeia* in these lakes, particularly for Cayuga and Seneca Lakes that have had quagga mussels for a longer time period. I also expected dreissenid impacts to be higher for oligotrophic lakes with a lower supply of food and shallow lakes with less suitable thermal habitat for *Diporeia*.

MATERIALS AND METHODS

Benthic sampling

My most recent sampling of profundal benthic communities in the New York Finger Lakes was from August-November 2010 using a petite Ponar grab (area sampled per grab 0.023 m^2). Canandaigua and Keuka Lakes were sampled on August 28 and 29, Skaneateles Lake on October 13, and Owasco and Seneca Lakes were sampled on November 11 and 12, 2010. Triplicate samples were collected at three to six different depths in each lake (Figure 2.1). The sediment collected was sieved through a 500 um sieve on the boat, and remaining material was preserved in 85% ethanol. All benthic organisms were sorted, identified and enumerated in the lab.

Historical data for profundal benthic communities of Keuka, Skaneateles, and Owasco Lakes is scarce. However, I can compare the 2010 data to my previous sampling of Skaneateles Lake in 2006 and Owasco Lake from 2006-2007. In June and July 2006, I conducted exploratory sampling of the two lakes using a petite Ponar grab, with a total of 21 grabs taken in Skaneateles Lake and 14 grabs in Owasco Lake (Figure 2.1). In 2007, I conducted a lake-wide benthic survey of Owasco Lake on June 10 and October 4 using a standard Ponar grab (area sampled per grab 0.05 m^2). Triplicate grabs were collected at 10 sites along a north-south transect. Sites were distributed every 10 m depth both north and south of the 50 m deep central basin. The

transect was resampled in July 2007 and June 2008 using a petite Ponar grab. In total, 124 grabs were collected from Owasco Lake during 2007 and 2008 (Figure 2.1).

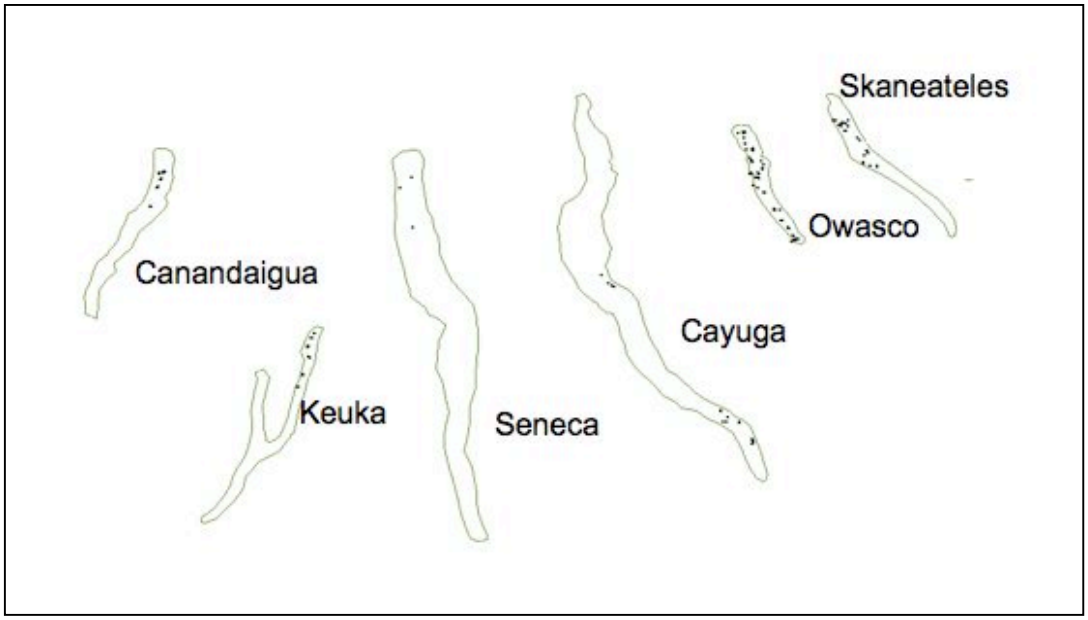


Figure 2.1. Benthic sampling sites during 2006-2010 in the six deepest New York Finger Lakes.

Canandaigua, Cayuga, and Seneca Lakes have been sampled extensively in the past, starting with Birge and Juday's sampling of the three lakes in 1918 with an Ekman dredge (Birge and Juday (1921, area sampled per grab 0.05 m^2). Canandaigua Lake was the subject of lake-wide benthic surveys (Ekman dredge) in 1927 and 1974 (Eaton et al. 1975). Cayuga Lake was sampled in 1952-53 (orange peel dredge, Henson 1954), 1964 (Ekman dredge, Green 1965), and July 1994 and 2001 (Ekman dredge, Dermott et al. 2006). Seneca Lake was sampled in August 2001 (Ekman dredge, Dermott et al. 2006).

My sampling of Cayuga Lake spanned from 2006-2009. In 2006, I conducted exploratory sampling at five sites near the northern end (Long Point State Park) and 12

sites near the southern end (south of Myers Point, Figure 2.1). In 2007, I began sampling a 100 m site west of Myers Point (43.372 N, 79.353 W) that had been sampled monthly throughout 1964 (Green 1965). In 2008-2009, I collected triplicate petite Ponars each month at two sites (40 and 80 m depth) near this location. The substrate at the three sites is rich in coarse terrestrial organic matter such as leaf litter due to a location near the inflow of Salmon Creek. In total 57 grabs were collected offshore of Myers Point from 2007-2009. For the 2008 data at the 80 m site, length (mm) of *Diporeia* and *Dreissena* from Cayuga Lake were measured using a digital camera connected to a dissection microscope and image analysis software.

Fatty acid analysis provided information on overall condition and diet of *Diporeia*. I measured the fatty acid composition of individual field collected *Diporeia* in the laboratory of Dr. Mark Teece at SUNY-ESF. Specimens from Cayuga and Owasco Lake were selected for comparing *Diporeia* populations living in direct contact with quagga mussels (Cayuga) with *Diporeia* populations with little contact with mussels (Owasco). In June 2008, I collected individuals from each population from sites of 35 m depth. Surface sediments at the 35 m site on the northern end of Owasco Lake had little coarse organic matter, while the Cayuga Lake site off of Myers Point had abundant coarse terrestrial organic matter (leaf litter). Substrates were also collected for fatty acid analysis. Individual *Diporeia* were flash frozen soon after collection and then freeze-dried. A 2:1 mixture of chloroform and methanol was used for the extraction of fatty acids. Gas chromatography (Shimadzu GC 17-A) separated and measured the mass of specific fatty acids relative to an internal C23 lipid standard. These measurements could therefore be converted to units of lipids as percentage of total dry weight. The specific fatty acid data is presented here as proportion of total lipids.

RESULTS

Dreissenid abundance in the New York Finger Lakes, 2010

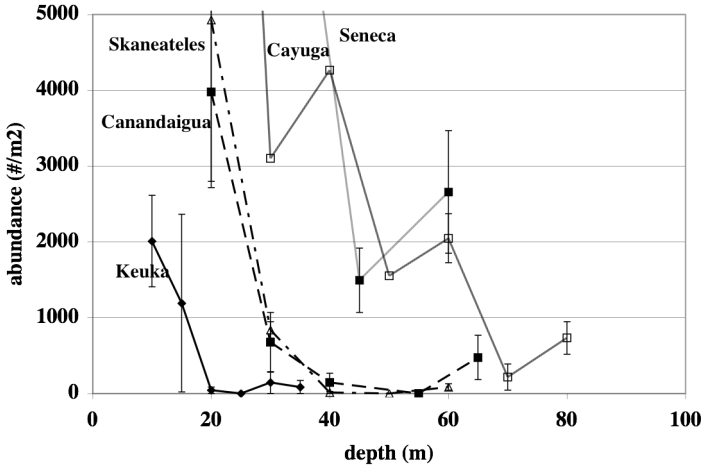
By 2010, quagga mussels were established in five out of the six deep Finger Lakes and outnumbered zebra mussels. Cayuga and Seneca Lakes had the highest abundances of quagga mussels, exceeding 1000/m^2 as deep as 60 m (Figure 2.2a, Table 2.2). In Canandaigua and Skaneateles Lakes, quagga mussels were abundant at 20 m depth (3980/m^2 and 4928/m^2) but decreased to 100/m^2 by 40 m. In Keuka Lake, quagga mussels were abundant at 10 m but were rare at depths > 15 m. Zebra mussels were rare in the five lakes in 2010 (Figure 2.2b, Table 2.2.).

Owasco Lake was the one study lake out of six without quagga mussels. Zebra mussels were most abundant at 10 m depth averaging 5287/m^2 (Figure 2.2c, Table 2.2). Zebra mussels were collected at low (< 300/m^2) densities at deeper sites, often clumped together as druzes on top of fine sediments.

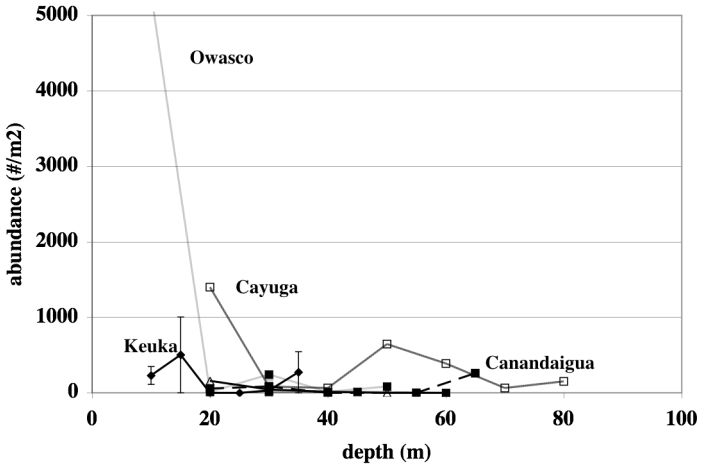
Diporeia abundance in the New York Finger Lakes, 2010

Diporeia were not found at depths < 10 m in all six study lakes. *Diporeia* were collected from most sites deeper than 15 m, although they were notably rare from a 20 m site in Cayuga Lake and a 30 m site in Seneca Lake (Figure 2.2c, Table 2.2.). *Diporeia* abundance at 20 m depth for the other four lakes was similar at 1000/m^2. *Diporeia* abundance increased with depth in Cayuga, Seneca, and Owasco Lakes, remained constant in Canandaigua and Keuka Lakes, and decreased with depth in Skaneateles Lake (Figure 2.2c, Table 2.2).

(a)



(b)



(c)

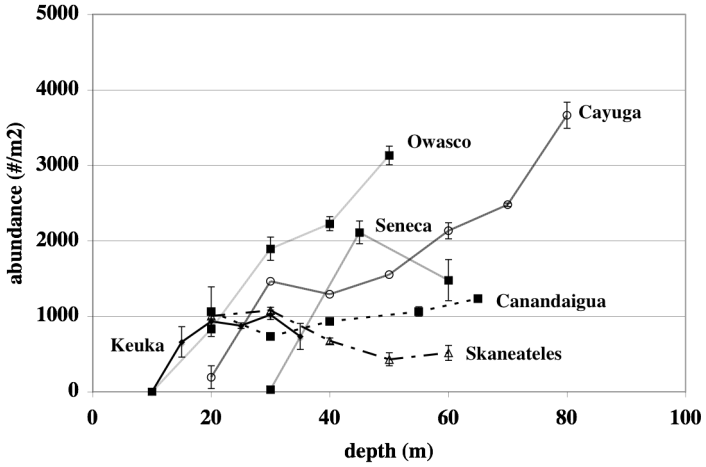


Figure 2.2. Abundance of a) quagga mussels (*D. rostriformis bugensis*), b) zebra mussels (*D. polymorpha*) and c) the amphipod *Diporeia* in the six Finger Lakes in 2010. Error bars represent one standard error.

Table 2.2. Average abundance of *Diporeia* and *Dreissena* spp. in 2010 for sites in the six Finger Lakes (#/m^2) with one standard error (n=3).

Lake	Depth m	n	*Diporeia*	s.e.	Quagga Mussels	s.e.	Zebra Mussel	s.e.
Keuka	10	3	0	0	2011	603	230	118
Aug 2010	15	3	661	200	1192	1171	503	503
	20	3	934	94	43	43	0	0
	25	3	876	38	0	0	0	0
	30	3	1020	63	144	144	29	29
	35	3	733	172	86	86	273	273
Owasco	10	3	0	0	0	0	5287	1745
Nov 2010	20	3	833	52	0	0	14	14
	30	3	1896	155	0	0	244	244
	40	3	2227	94	0	0	14	14
	50	3	3132	123	0	0	86	43
Canandaigua	20	3	1063	329	3980	1265	57	38
Aug 2010	30	3	733	0	675	395	86	66
	40	3	934	14	144	123	0	0
	55	3	1063	63	0	0	0	0
	65	3	1236	14	474	293	259	237
Skaneateleles	20	3	1006	38	4928	2129	158	137
Oct 2010	30	2	1078	43	840	108	43	43
	40	3	675	38	14	14	14	14
	50	3	431	86	0	0	0	0
	60	3	517	100	86	43	0	0
Seneca	30	3	29	29	10229	2643	14	14
Nov 2010	45	3	2112	151	1494	424	14	14
	60	3	1480	273	2658	809	0	0
Cayuga	20	2	194	151	17843	5129	1401	1013
Jun-Jul 2006	30	1	1465		3103		86	
	40	2	1293	914	4267	3405	65	65
	50	1	1552		1552		647	
	60	2	2133	108	2047	323	388	43
	70	2	2478	22	216	172	65	22
	80	2	3664	172	733	216	151	108

Comparison to 2006-2007, Owasco and Skaneateles Lakes

Some changes in the dreissenid and *Diporeia* populations in Skaneateles and Owasco Lakes are evident when comparing my 2010 data with data from 2006-2007. Skaneateles Lake had no quagga mussels in 2006. In that year, zebra mussels were collected at relatively low abundances and only in shallow habitats (590/m^2 at 20 m depth). By October 2010, quagga mussels had colonized Skaneateles Lake and outnumbered zebra mussels- at the same depth quagga mussel abundance was 4928/m^2 while zebra mussel abundance was 158/m^2. Quagga mussels had also expanded to 30 m depth, averaging 840/m^2. Despite the establishment of quagga mussels, *Diporeia* abundance had not significantly changed since 2006 and still decreased with depth (Figure 2.3a). In 2006, Owasco Lake had zebra mussels at shallow sites and no quagga mussels as observed in 2010. Despite similar levels of dreissenids, *Diporeia* abundance in the deepest part of the lake was lower in 2006 and 2007 than in 2010 (Figure 2.3b).

Relationship of Diporeia and dreissenid abundance in 2010

Sites from 20 to 45 m depth in the six lakes were selected as suitable thermal habitat for *Diporeia* where they also were most likely to be in direct contact with dreissenids. For these sites, the abundance of *Diporeia* was not correlated with the abundance of dreissenids in 2010 (Figure 2.4). *Diporeia* abundance in four of the six lakes (Cayuga, Seneca, Skaneateles, and Canandaigua) were >1000/m^2 despite direct contact with quagga mussels at levels >1000/m^2. However, *Diporeia* abundance was low (<200/m^2) in the two sites with very high levels (>10,000/m^2) of quagga mussels in Seneca and Cayuga Lakes.

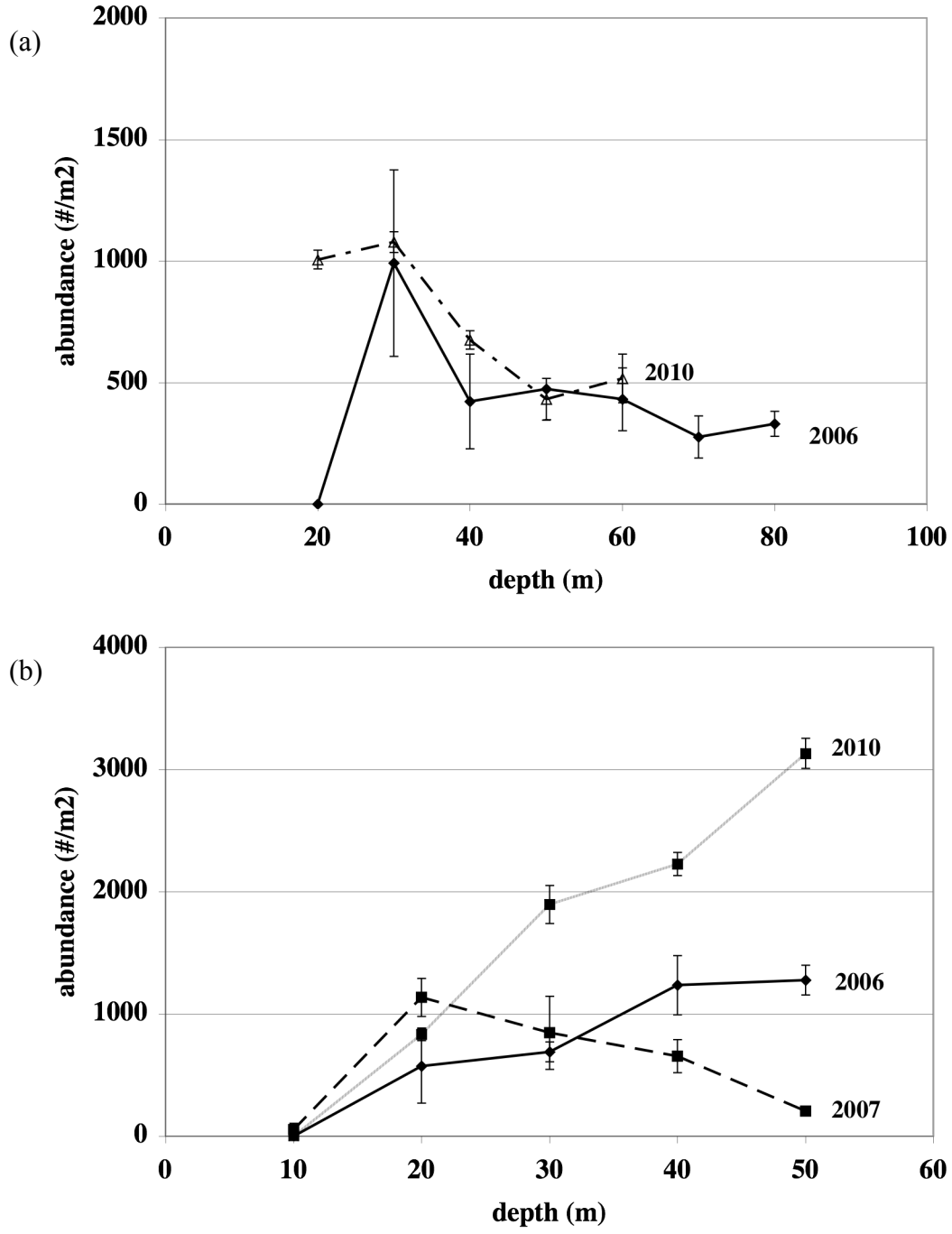


Figure 2.3. Abundance of *Diporeia* in Skaneateles in 2006 and 2010 (a) and Owasco Lake in 2006, 2007, and 2010 (b). The 2007 data for Owasco Lake is based on collections during June, July, and October. Error bars represent one standard error.

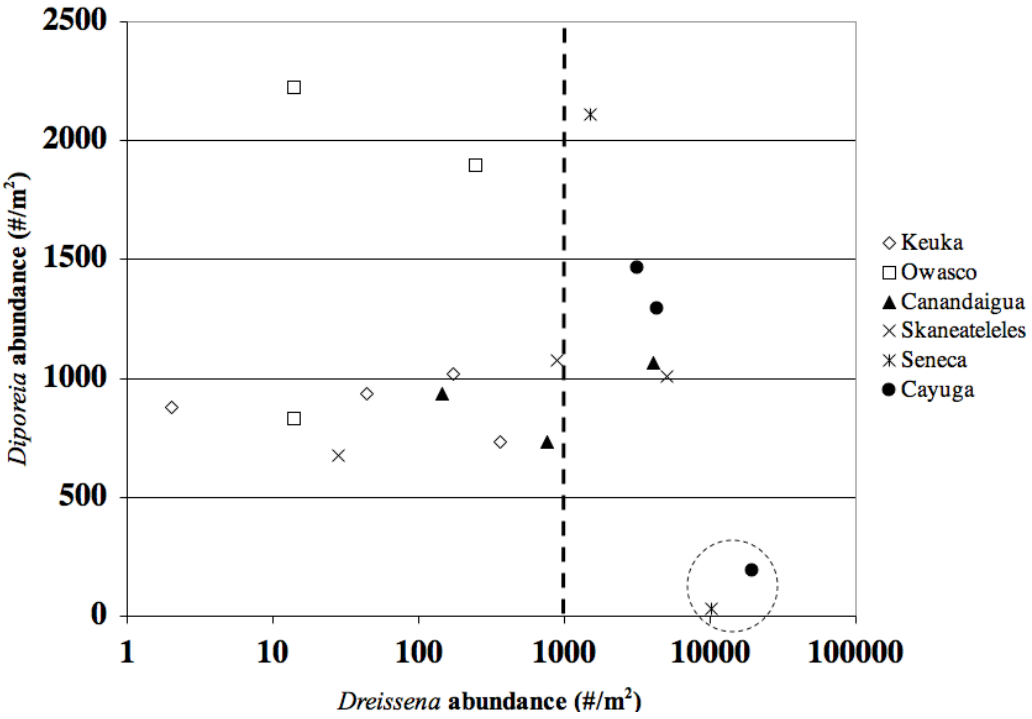


Figure 2.4. Abundance of *Diporeia* and *Dreissena* in six Finger Lakes at sites from 20-45 m depth during 2010. Dashed line marks dreissenid density of 1000/m^2 at which effects on *Diporeia* have been seen in the Great Lakes. Circle marks two sites in Cayuga and Seneca Lakes where *Diporeia* abundances are low at dreissenid levels > 10,000/m^2.

Diporeia associated with terrestrial organic matter in Cayuga Lake

Diporeia abundances were particularly high within the organic rich substrate off of Myer's Point in Cayuga Lake in 2007-2009. *Diporeia* abundance averaged 3530/m^2 (s.e. 708) at 40 m, 7865/m^2 (s.e. 519) at 80 m, and 7215/m^2 (s.e. 724) at 100 m. Quagga mussel abundance was also high at these sites averaging 4201/m^2 (s.e. 770) at 40 m, 3228/m^2 (s.e. 429), and 681/m^2 (s.e. 409) at 100 m. The size distribution of *Diporeia* at the 80 m site consisted of two size cohorts at 2 mm and 6 mm length corresponding to young-of-year and adult age classes (Figure 2.5b). The 2 mm cohort was most abundant in June, indicating a release of young in early spring. From June to October 2008, the 2 mm cohort grew to 3 mm, a growth rate of 0.25 mm per month.

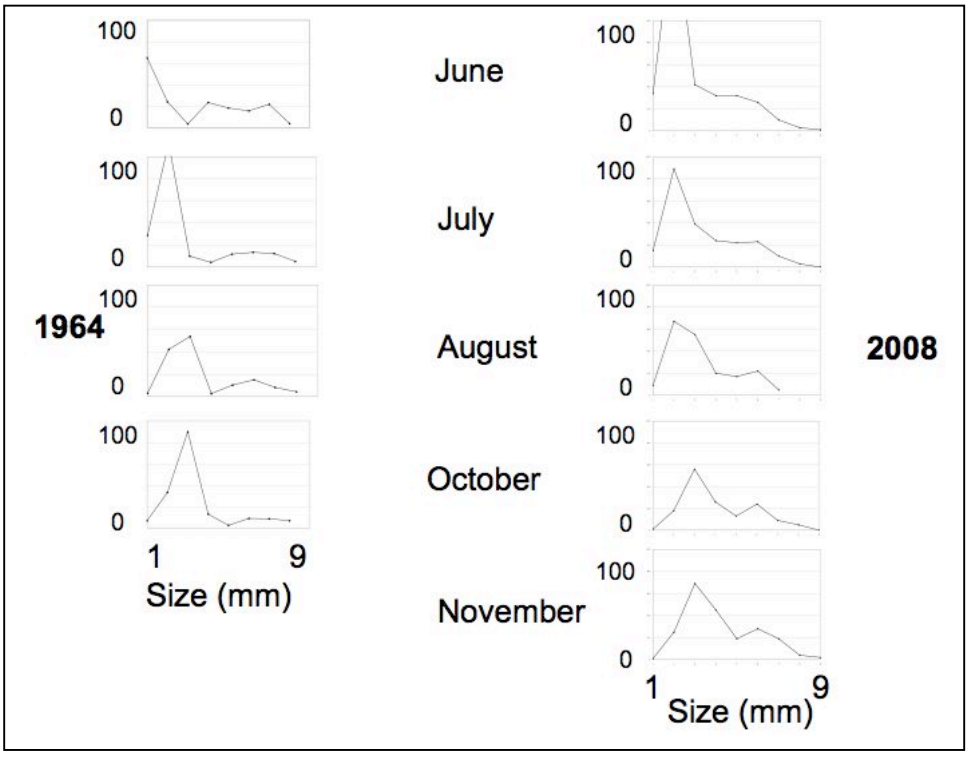


Figure 2.5. Monthly size distribution of *Diporeia* at 80 m depth in Cayuga Lake off of Myer's Point in 1964 (Green 1965) and 2008 (this study). Y-axis is individuals per grab.

Quagga mussels also had two size defined cohorts, at 5 mm and 20 mm that were present throughout the sampling period (Figure 2.6).

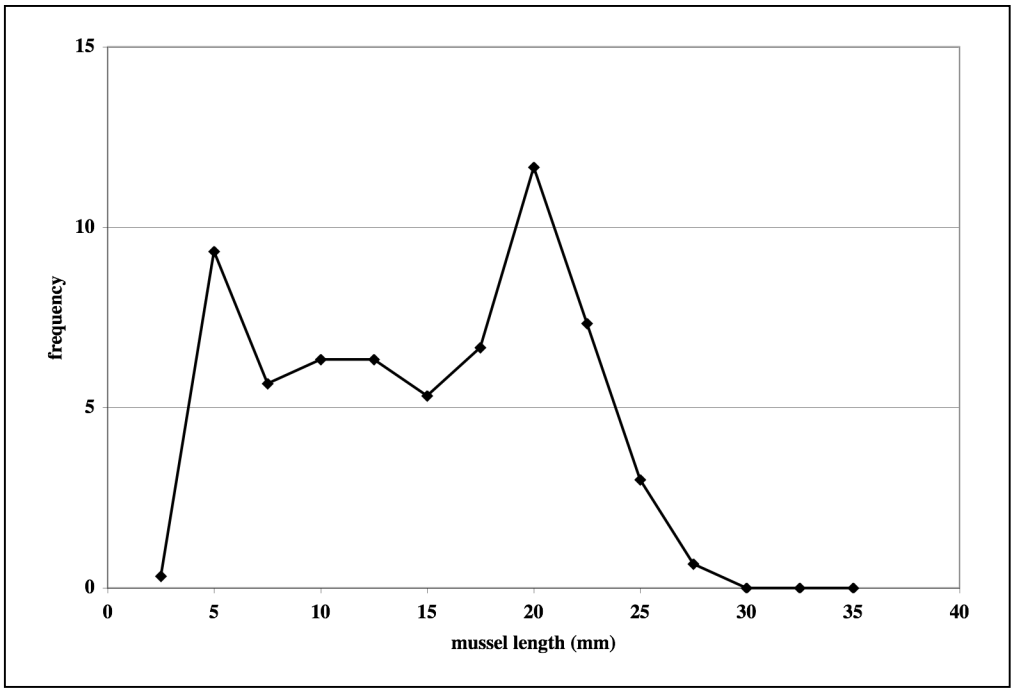


Figure 2.6**.** Size distribution of quagga mussels in Cayuga Lake at 80 m depth on September 25, 2008. Note peaks at 5 and 20 mm size classes. Y-axis is individuals collected in a single grab.

Condition of Diporeia in Owasco and Cayuga Lakes

Individual adult *Diporeia* (7-8 mm in size) from Owasco Lake had higher dry weight and lipid content than *Diporeia* from Cayuga Lake. The dry weight of similar sized adult *Diporeia* from Owasco Lake was 2.12 mg (s.e. 0.13) relative to 0.65 mg (s.e. 0.07) of *Diporeia* from Cayuga Lake. Owasco *Diporeia* were also richer in lipids (51.6% of dry weight, s.e. 3.1%) than Cayuga Lake *Diporeia* (14.9% of dry weight, s.e. 3.3%). The specific lipid composition also differed for the two populations (Table

2.3). Saturated fatty acids (SAFA), primarily palmitic acid (16:0), composed approximately 15% of the fatty acids of *Diporeia* in both lakes. Monounsaturated fatty acids (MUFAs) were 50.4% of the fatty acids of Owasco Lake *Diporeia* and 41.7% of those from Cayuga Lake. The common MUFA oleic acid (18:1w9) was a primary fatty acid in both populations, approximately 22%. Owasco *Diporeia* were particularly rich in the MUFA palmitoleic acid (16:1w7). Approximately 5% of the fatty acids in *Diporeia* from both lakes were diunsaturated fatty acids (DUFAs), particularly lineolic acid (18:2w6), a precursor to essential fatty acids.

Table 2.3. Fatty acid composition of *Diporeia* from Cayuga and Owasco Lakes in terms of percentage of total lipid composition.

	Cayuga average	**(n=8)** s.e.	**Owasco** average	**(n=8)** s.e.	**Significant?**
Saturated Fatty Acids (SAFA):					
14:0	0.3	0.2	2.2	0.8	Yes, O>C
'16:0	14.6	1.9	17.1	0.8	No
'18:0	3.9	0.6	1.1	0.1	Yes, C>O
Sum of SAFA =	**18.7**	**2.0**	**20.4**	**1.4**	No
Monounsaturated Fatty Acid (MUFA):					
14:1	0.1	0.1	1.7	0.6	Yes, O>C
'16:1w7	7.8	1.9	22.5	0.7	Yes, O>C
'16:1w9	0.7	0.3	0.4	0.0	No
18:1w7	11.0	4.4	1.9	0.5	No
18:1w9	22.0	4.8	23.9	0.6	No
Sum of MUFA =	**41.7**	**1.7**	**50.4**	**0.6**	Yes, O>C
Diunsaturated Fatty Acid (DUFA):					
18:2w6	6.6	1.0	4.5	0.6	No
Sum of DUFA =	**6.6**	**1.0**	**4.5**	**0.6**	No
Polyunsaturated Fatty Acid (PUFA):					
18:3w3	2.6	0.2	2.3	0.1	No
18:4w3	1.6	0.3	4.1	0.3	Yes, O>C
20:4w6 ARA	5.0	1.0	1.7	0.1	Yes, C>O
20:5w3 EPA	15.6	1.1	10.9	0.5	Yes, C>O
22:6w3 DHA	8.1	2.0	5.8	0.4	No
Sum of PUFA =	**32.9**	**3.7**	**24.7**	**1.1**	Yes, C>O
Dry Weight of *Diporeia* (mg)	**0.65**	**0.07**	**2.12**	**0.13**	

Polyunsaturated fatty acids (PUFAs) essential for growth were 32.9% of the fatty acids in Cayuga *Diporeia* and 24.7% of those extracted from Owasco *Diporeia*. Essential fatty acids eicosapentaeonic acid (EPA, 20:5w3) and docosahexaenoic acid (DHA, 22:6w3) were the two most prominent PUFAs. Overall, Owasco *Diporeia* had a higher proportion of MUFAs, while Cayuga *Diporeia* had a higher proportion of PUFAs.

Owasco Lake surface sediment was only 0.005% lipid. Sediments at our Myer's Point sites in Cayuga Lake were rich in terrestrial organic matter, averaging 1452 g dry weight (DW)/m^2 at 40 m and 862 g DW/m^2 at 80 m. This material was 0.1% lipid, nearly 20 times more lipid rich than Owasco Lake sediments. The Cayuga organic matter was low in palmitoleic acid (16:1w7), while high in the PUFA EPA relative to the Owasco substrate.

DISCUSSION

Replacement of zebra mussels by quagga mussels in the Finger Lakes

Quagga mussels are replacing zebra mussels in both the Great Lakes and in their home range (Nalepa et al. 2009, Watkins et al. 2007, Karatayev et al. 1998). I show that this is also occurring in the Finger Lakes of central New York. Both species feed on phytoplankton, but the lower respiration rates of quagga mussels provide them with a competitive advantage when food resources are low (Stoeckmann 2003). Quagga mussels are also thought to better tolerate high turbidity and low oxygen levels. In Seneca and Cayuga Lakes, the two Finger Lakes that have had quagga mussels since 1994, quagga mussels are abundant as deep as 60 m. This expansion of quagga mussels to deep habitats mirrors the trend seen in lakes Ontario, Michigan, and

Huron. Quagga mussel expansion to deep habitats in many lakes of North America reflects a tolerance of low water temperatures and soft substrates.

Persistence of Diporeia in the Finger Lakes

Despite the expansion of quagga mussels, populations of the amphipod *Diporeia* persist in the six deepest Finger Lakes. Although Owasco Lake has only shallow zebra mussels and Keuka Lake has relatively low levels of quagga mussels, *Diporeia* was found in direct contact with quagga mussels at levels > 1000/m^2 for the four other lakes. In contrast, for the Laurentian Great Lakes, *Diporeia* populations at intermediate depths declined at a time when levels of dreissenids were < 1000/m^2 (Nalepa et al. 2009). Genetic differences are not responsible, as Finger Lake *Diporeia* are genetically similar to those of Lake Ontario, Michigan and Huron (although distinct from *Diporeia* of Lake Superior, Pilgrim et al. 2009). *Diporeia* populations in the New York Finger Lakes tolerate much higher (up to 10,000/m^2) levels of dreissenids than Great Lakes *Diporeia*.

Diporeia abundance associated with trophic state

Overall lake productivity was more important than mussel abundance in determining *Diporeia* abundance in the Finger Lakes. For example, the low abundance (1000/m^2) of *Diporeia* in Skaneateles Lake is consistent with the very low productivity of the lake. Skaneateles Lake has the lowest levels of average (May-October in the epilimnion) total phosphorus (TP, 4 μg/L) and chlorophyll (chl *a,* 0.7 μg/L) and the deepest secchi depth (7.6 m) of all eleven Finger Lakes (Callinan 2001, Table 2.1). In the late 1970s the lake had slightly higher values for average TP (6.1 μg/L) and chl *a* (1.95 μg/L), and a shallower secchi depth (6.6 m). These parameters reflect a long-term oligotrophic state comparable to the current trophic state of the

offshore of the Great Lakes excluding Lake Erie. *Diporeia* abundance decreased with depth in both our samplings of Skaneateles Lake in 2006 and 2010.

Diporeia abundance was also relatively low in Canandaigua and Keuka Lakes, but did not decrease with depth. Canandaigua Lake is nearly as oligotrophic as Skaneateles Lake, with similar values of TP (6.2 μg/L) and chl *a* (1.0 μg/L) (Callinan 2001). The abundance of *Diporeia* in Canandaigua Lake has been stable for nearly a century- my measurements from 2010 (average 1006/m^2) are very comparable to that measured in 1918 (911/m^2, Birge and Juday 1921), 1927 (1066/m^2, Eaton unpublished), and 1974 (1193/m^2, Eaton et al. 1975). Keuka Lake is more mesotrophic with higher TP (8.0 μg/L) and chl *a* (2.8 μg/L), and lower transparency (5.6 m secchi depth), yet had relatively low *Diporeia* abundance.

The higher abundance (2000-3000/m^2) of *Diporeia* in Cayuga, Seneca, and Owasco Lakes is consistent with the more mesotrophic state of the three lakes. The three lakes have higher average levels of TP (9.7, 9.8, and 12.0 μg/L) and chl *a* (3.5, 2.4, and 3.8 μg/L) as well as lower transparency (4.0, 6.0, and 2.8 m secchi depth) than Skaneateles and Canandaigua Lakes (Callinan 2001). A difference in trophic state implies that there is more food available for *Diporeia* in the three lakes. A similar relationship of *Diporeia* abundance and productivity has been observed within a single lake (New York State's Lake George) along a productivity gradient from the mesotrophic south end to the more oligotrophic north end (Siegfried 1985). Prior to the recent decline, *Diporeia* abundance in the Great Lakes was also correlated with overall productivity with Lake Superior having the fewest *Diporeia* and Lake Michigan and Lake Ontario having more abundant populations (Cook and Johnson 1974). The relationship does not extend to eutrophic lakes. *Diporeia* population declines in Round Lake (Ontario), Lac Memphremagog (Quebec), and lakes

Champlain and Winnipeg have been attributed to eutrophication rather than dreissenid introduction (Dermott et al. 2005).

Alternate food resources for Diporeia in Cayuga Lake

Although persistence of *Diporeia* in most of the Finger Lakes could be due to low abundances of deep-water quagga mussels, *Diporeia* in Cayuga and Seneca Lakes coexist with abundant quagga mussels at levels near 1000-5000/m^2. This finding is contrary to the hypothesis that competition for the spring diatom bloom is important for the decline in *Diporeia* in the Great Lakes unless competition is mitigated by other food resources. Our fatty acid analysis indicates that *Diporeia* of Cayuga Lake are feeding on food resources other than diatoms.

Owasco *Diporeia* were in better condition with a much higher lipid content (51.6% relative to 14.9%) than Cayuga *Diporeia*. The high lipid content of Owasco Lake *Diporeia* suggests that this population has high food availability and perhaps benefits from lower lake-wide levels of dreissenids. The lipid content of Cayuga *Diporeia* is lower than in Owasco Lake and healthy *Diporeia* populations from Lake Michigan collected in 1989 (21.7%, Cavaletto et al. 1996), but comparable to that of *Diporeia* from Charleston Lake, Ontario in 2006 (13.7%, Kainz et al. 2010). Although lower than the 33.1% lipid content measured from Cayuga *Diporeia* in June, 1964 (Green 1971), our 2008 size distribution data indicates that the population is still successfully reproducing. The growth rate of *Diporeia* in 2008 calculated from our cohort analysis is also similar to the growth rate measured in 1964 of 0.33 mm per month (Figure 2.5, Green, 1965).

High proportions of the essential fatty acids, particularly EPA and DHA, indicate that Owasco and Cayuga *Diporeia* have high quality diets. Levels of other fatty acids represent dietary tracers. *Diporeia* in Owasco Lake were particularly rich

in the MUFA palmitoleic acid (16:1w7), an indicator of diatom consumption (Goedkoop et al. 2000). Clearly, the zebra mussels in Owasco Lake are not eliminating diatoms as a food source for *Diporeia*. The lower content of this diatom tracer in Cayuga *Diporeia* suggests a greater reliance on detritus. Diatoms are also a primary source of the PUFA EPA, so it is interesting that despite having low levels of the diatom tracer, the proportion of EPA in Cayuga *Diporeia* (15.6%) was significantly higher than that of Owasco *Diporeia* (10.9%). However, this may be because the fatty acid content of coarse terrestrial organic matter from Cayuga sediments was high in EPA but low in the diatom tracer. Also note that Owasco *Diporeia* had a 50% greater absolute content of EPA (mg/g DW) than Cayuga *Diporeia*.

Other potential food web tracers were less clear-cut. Fatty acids with odd numbers of carbon in their chains (e.g. 17:0) and vaccenic acid (18:1w7) have been used as markers for bacterial activity (Parrish et al. 2000, Goedkoop et al. 2000). Although Cayuga *Diporeia* had a higher proportion of vaccenic acid than Owasco *Diporeia*, the difference was not significant, and no odd number carbon chains were detected. Levels of the fatty acids 18:2w6 and 18:3w3, indicators of terrestrial plant matter, were also not significantly different for the two populations. *Diporeia* in both lakes exceeded the 2.5% threshold assigned to this indicator (Parrish et al. 2000). Therefore, the diatom tracer 16:1w7 emerges as the most consistent indicator of different trophic roles for *Diporeia* in the two lakes.

Thus the coexistence of *Diporeia* and quagga mussels in Cayuga Lake is not inconsistent with the hypothesis that *Diporeia* is declining in the Great Lakes due to competition with dreissenid mussels, in particular quagga mussels, for the spring diatom bloom. Fatty acid biomarkers indicate that Cayuga *Diporeia* are less dependent on deposited diatoms than *Diporeia* from Owasco Lake that has only zebra

mussels. Cayuga Lake *Diporeia* have access to an alternative food in detritus of terrestrial origin that enables the amphipod to maintain sufficient condition for growth and reproduction. The future response of *Diporeia* populations in oligotrophic Skaneateles and Canandaigua Lakes to quagga mussel expansion to deep habitats may provide additional insight towards understanding the disappearance of *Diporeia* in the Great Lakes.

Higher threshold for coexistence with quagga mussels

Diporeia abundance was suppressed at shallow (20-30 m) sites in Seneca and Cayuga Lakes where dreissenid abundance exceeded 10,000/m^2. This change is evident when comparing my data with earlier studies of Seneca Lake. In 2001, *Diporeia* abundance was 1280/m^2 and dreissenid mussel abundance was 2575/m^2 at 30 m depth in Seneca Lake (Dermott et al. 2005, Figure 2.7). *Diporeia* abundance had increased slightly from levels near 1110/m^2 in 1918 (Birge and Juday 1921). By 2010, quagga mussel abundance had reached 10,229/m^2 (s.e. 2643) and *Diporeia* had nearly disappeared (29/m^2 (s.e. 29) at this site. The response of *Diporeia* to only very high levels of quagga mussels suggests that factors other than competition for food contributed to the disappearance of *Diporeia* from this site.

Conclusions

In summary, *Diporeia* populations of the New York Finger Lakes in 2010 have shown few negative impacts from the establishment of dreissenid mussels in these lakes since the 1990s. This persistence applies to six deep lakes that cover a wide range of productivity and depth. Particularly interesting is *Diporeia*'s resiliency despite living in direct contact with abundant (>1000/m^2) quagga mussels in four of the six lakes (Cayuga, Seneca, Skaneateles, Canandaigua). Few examples of

coexistence of the two organisms exist in the Great Lakes as *Diporeia* populations steadily disappear. The findings of the Finger Lake benthic surveys suggest that dreissenids may not be contributing to the decline of *Diporeia* in the Great Lakes. If dreissenids have caused the decline of *Diporeia* in the Great Lakes, potential reasons for *Diporeia* of the Finger Lakes persisting include 1) dreissenids of the Finger Lakes have not transported pathogens, 2) dreissenid filter feeding in the deep Finger Lakes has not intercepted supply of diatoms to *Diporeia*, 3) alternative food sources exist in the Finger Lakes such as terrestrial organic matter, and 4) *Diporeia* of the Finger Lakes are in better condition and thus more resistant to dreissenid impacts.

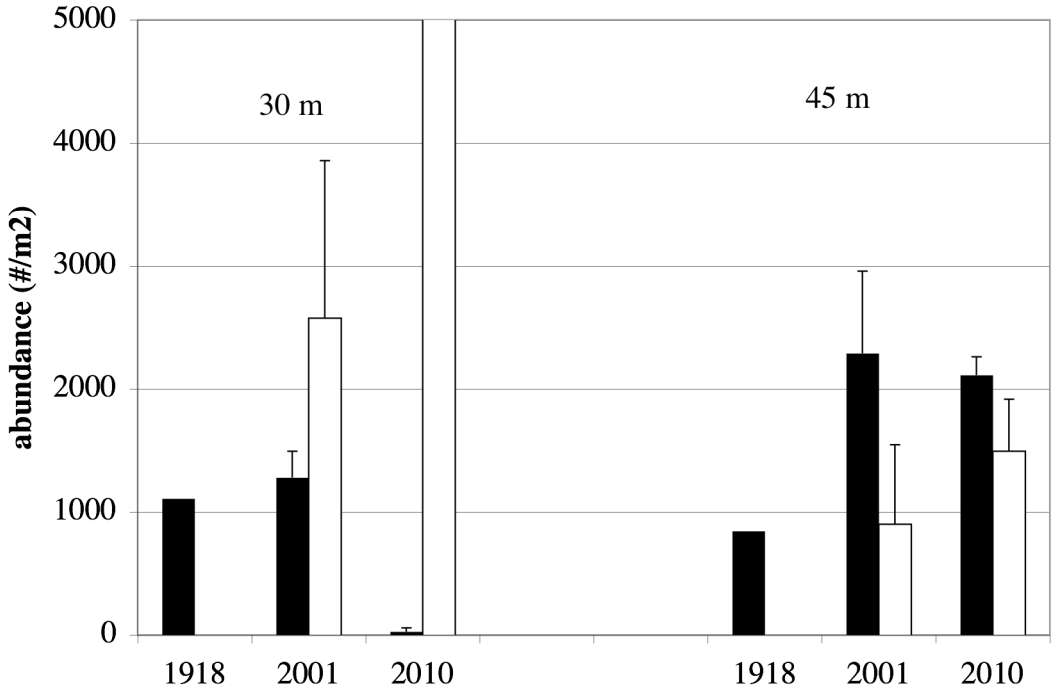


Figure 2.7. *Diporeia* (dark bars) and dreissenid (white bars, sum of zebra and quagga mussels) abundance (individuals/m^2) at 30 and 45 m in Seneca Lake for 1918, 2001, and 2010. The site locations for 2001 and 2010 are the same. Error bars are one standard error (N=4 for 2001, N=3 for 2010).

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CHAPTER 3: EVALUATING THE ROLE OF DREISSENID-BORNE PATHOGENS IN THE DISAPPEARANCE OF *DIPOREIA* IN THE GREAT LAKES

ABSTRACT

The disappearance of the native benthic amphipod *Diporeia hoyi* from large areas of the Great Lakes has been associated with the expansion of exotic dreissenid mussels, particularly the spread of quagga mussels (*Dreissena rostriformis bugensis*) to deep profundal habitats. One possible mechanism is that quagga mussels act as a vector for pathogens that are deadly to *Diporeia*. Pathogen transfer could occur during direct contact of the two organisms or indirectly by water exchange. I evaluated this hypothesis in a series of 28-day microcosm experiments combining *Diporeia* and quagga mussels from different large lakes at abundance levels of 2000/m^2. Laboratory survival of Great Lake *Diporeia* populations at risk (Lake Huron) and stable (Lake Superior) were not significantly affected by exposure to quagga mussels from Lake Michigan or Cayuga Lake (New York Finger Lake) relative to no-mussel controls (ANOVA, p=0.76 and p=0.84 respectively). Laboratory survival of *Diporeia* from Cayuga Lake was also not significantly affected by exposure to quagga mussels from Lake Michigan relative to no-mussel controls (Student's t-test, p=0.50). Even when elevating quagga mussel abundance levels to 10,000/m^2, laboratory survival of *Diporeia* from Cayuga Lake was not affected (p=0.37). These findings indicate that it is not likely that quagga mussels have contributed to the decline of *Diporeia* by acting as a vector for harmful pathogens.

INTRODUCTION

Pathogens are recognized as forces that can reduce host populations. Many aspects of the decline of the benthic amphipod *Diporeia* that began in the mid-1990s in many of the Great Lakes are consistent with the role of a pathogen. Amphipod populations at shallow sites disappeared very quickly- sometimes in the span of months. The *Diporeia* populations at these sites were extremely dense (>10,000/m^2), a factor that could have facilitated the spread of a pathogen. *Diporeia* declines first occurred in Lake Erie and Lake Ontario, and then took place in Lake Michigan and Lake Huron. In theory, epidemics end due to a reduction of the host population and/or the immunity of surviving individuals (Anderson and May 1986). The continued decline of *Diporeia* suggests that if a pathogen is involved, it is driving itself and the amphipod toward extinction.

The pioneering study of Messick et al. (2004) provided the first evidence that *Diporeia* are vulnerable to a number of metazoan parasites and microorganisms. Ciliates were a common parasite of *Diporeia*, prevalent in 37% of the 1715 amphipods collected from Lakes Michigan and Huron. However, this external parasite induced little harm on its amphipod host. On the other hand, intracellular infection by a rickettsia-like microorganism led to a clear host response- hypertrophy of adipose cells, hemocytes, and epithelial cells of the gut- but was found in only 1.6% of the specimens. Similar infections have been implicated in die-offs of the freshwater amphipod *Crangonyx floridanus* in Florida (Frederici et al. 1974). Microsporidians, a common and serious pathogen of crustacean hosts (Meyers 1990), were found in 3.8% of the specimens. Epidemics of water molds (e.g. *Metschnikowia*-type yeasts) commonly crash populations of the freshwater cladoceran *Daphnia*, but these molds are very rare (< 0.05%) in *Diporeia* (Messick et al. 2004, Kiziewicz and Nalepa 2008). This inverse relationship of virulence and infection rate is consistent with theoretical

studies that have predicted that parasites that greatly reduce host survival and fecundity will have low equilibrium infection rates (Anderson and May 1981). Therefore, although virulent pathogens were rare in *Diporeia*, amphipod populations could be reduced in epidemics.

Mortality due to parasitism can increase when the host is under environmental stress, particularly in the case of temperature. For example, an 80 ha bed of the amphipod *Corophium volutator* vanished in five weeks in the spring of 1990 in the Wadden Sea off the coast of Denmark due to parasitism by the trematode *Maritrema subdolum* (Mouritsen and Jensen 1997). Water temperatures were 3-5°C above normal in the two months prior to the event. The study attributed the high mortality to increased transmission of the parasite to the amphipod from snail secondary hosts. Associations of higher parasite-induced mortality with higher temperatures have led to predictions of increased disease risk and even extinctions of marine and terrestrial organisms due to global warming (Harvell et al. 2002, Mouritsen et al. 2005).

For the Great Lakes ecosystem, rapid temperature changes rather than high temperatures contribute to most outbreaks of disease. For example, several emerging fish diseases such as Viral Hemorrhagic Septicemia Virus (VHSV, Bain et al. 2010) and Spring Viremia Carp Virus (SVCV) typically occur at times of rapid change in temperature (i.e. spring or fall). The mortality rate of VHSV is highest at 3-12°C and rare > 15°C (McAllister 1990) and SVCV occurs at temperatures < 18°C. Similarly, bacterial coldwater disease (*Flavobacterium psychrophilica*) affecting salmonids has highest mortality rates from 4-10°C. In the case of *Diporeia*, shallow sites with water temperatures near the thermal tolerance (10°C) of this stenothermic species were the first to be affected. These sites are subject to high variation in water temperature. However, the decline has continued to deeper populations well below the thermocline with little temperature variation (4-6°C).

The role of exotic invertebrates and fish in carrying new pathogens to the Great Lakes ecosystem has not been confirmed. Field evidence in the Great Lakes consistently associates the expansion of dreissenid mussels, particularly quagga mussels (*Dreissena rostriformis bugensis*) to deepwater habitats, to the decline of *Diporeia* (Chapter 1). One possible mechanism is that quagga mussels act as a vector for pathogens that are deadly to *Diporeia*. Several highly pathogenic microbes including rickettsia-like organisms and *Flavobacterium* spp. have been identified within zebra mussels (*Dreissena polymorpha*) collected from water bodies within the Great Lakes Basin (Winters 2008). Although this mechanism should require direct contact of the two species, diseases could be carried via digestion products (pseudofeces) transported offshore from shallow mussel beds or be present even when quagga mussels are in such low densities that they are difficult to detect with standard sampling. However, my observations of co-occurring *Diporeia* and quagga mussels in the New York Finger Lakes (Chapter 2) suggest that if the pathogen hypothesis is correct then either a) the pathogen community associated with quagga mussels from the Great Lakes is more harmful than that from the Finger Lakes, or that b) *Diporeia* from the Finger Lakes are better able to survive exposure than those of the Great Lakes. Winters (2008) identified considerable variation in the microbial communities harbored by *Dreissena* from different water bodies, indicating that dreissenids from the Finger Lakes and Great Lakes could carry different pathogens affecting *Diporeia*. These observations led to four testable hypotheses:

Hypothesis 1: Indirect exposure to quagga mussels induces mortality in *Diporeia*.

Hypothesis 2: Direct exposure to increased levels of quagga mussels induces mortality in *Diporeia*.

Hypothesis 3: Exposure to quagga mussels from Cayuga Lake does not have the same impact on *Diporeia* as exposure to quagga mussels from the Great Lakes.

Hypothesis 4: *Diporeia* from Cayuga Lake are better able to survive exposure to quagga mussels than *Diporeia* of the Great Lakes.

My approach was to expose *Diporeia* to quagga mussels within experimental microcosms over extended exposure periods. These experiments are similar in design to earlier experiments that have evaluated the effect of different sediments on *Diporeia* survival (Gossiaux et al. 1993, Landrum et al. 2000, Dermott et al. 2005a). These previous studies tested sediments from a wide range of sites throughout the Great Lakes including degraded areas of concern (AOC), locations where *Diporeia* populations had declined, as well as pristine sites offshore with persisting populations. They tested the hypothesis that toxins (due to industrial pollution or dreissenid colonization) elevate *Diporeia* mortality. In fact, exposure to sediments from highly degraded areas did negatively affect *Diporeia* survival. For example, sediments from a site in Michigan's Saginaw River downstream of a wastewater treatment plant elevated mortality by 55% compared to control sediments for a 28-day test period (Gossiaux et al. 1993). Sediments from a nearshore site (Niagara Bar) in Lake Ontario also induced higher mortality (40%) in a similar study (Dermott et al. 2005a). However, these studies did not find significant decreases in survival when *Diporeia* were exposed to sediments from typical offshore habitats including sites colonized by dreissenids. Consequently, sediment toxicity has not been considered to be a primary cause for the *Diporeia* decline. I revisited the approach of Gossiaux et al. to evaluate

whether dreissenid mussels carry a pathogen community that is detrimental to *Diporeia*.

MATERIALS AND METHODS

Collection of Organisms

Live *Diporeia* and quagga mussels were collected in the Great Lakes during the Summer 2007, Spring 2008, and Summer 2008 surveys aboard the US Environmental Protection Agency (EPA) vessel R/V Lake Guardian. Additional organisms from Lake Michigan were collected aboard the Lake Guardian in September 2007 and other research vessels in June 2008. I also collected live *Diporeia* and quagga mussels using a small boat in Cayuga Lake during 2007-2009. All of the organisms were transported live to the Cornell Biological Field Station in Bridgeport, New York, USA. Table 3.1 lists the specific collections used in my exposure experiments.

One primary challenge in collecting specimens of *Diporeia* for this study was the rapidly declining populations of *Diporeia* in the Great Lakes. I did not include the deep eastern basin of Lake Erie in my project design due to known extirpation. Extremely low populations of *Diporeia* in Lake Ontario led me to abandon efforts to collect in this lake. In lakes Huron and Michigan, shallow populations of *Diporeia* disappeared (Nalepa et al. 2009), making collection from deep habitats necessary. The deep habitats, even in the absence of quagga mussels, were experiencing long term and significant *Diporeia* declines. In Lake Michigan, *Diporeia* populations at sites > 90 m depth declined from 4567/m^2 in 1995 to 2752/m^2 in 2000 to 1244/m^2 in 2005 (Nalepa et al. 2009). These lake-wide trends are consistent with observed trends at my individual sites. For example, *Diporeia* abundance at EPA Site 40 (170 m depth) in

Table 3.1. Collection sites of live *Diporeia* and *Dreissena* used in exposure experiments.

Diporeia

Lake	Site	Depth (m)	Date Collected	Location
Michigan	40	170	9/23/07	44.760N, 86.967W
	C-5	100	6/25/08	42.817N, 86.833W
Huron	54	124	4/19/08	45.517N, 83.417W
Superior	23B	62	8/18/07	46.597N, 84.807W
	MED 53	39	9/08/07	46.646N, 90.230W
Cayuga	Myers	40-60	several dates	43.372N, 79.353W

Dreissena rostriformis bugensis

Lake	Site	Depth (m)	Date Collected	
Michigan	52B	54	8/4/07	45.808N, 86.046W
	Muskegon	45	6/4/08	43.188N, 86.430W
Ontario	63	86	8/10/07	43.732N, 77.017W
	Mexico Bay	60	8/08	
Cayuga	Myers	40-60	several dates	43.372N, 79.353W

Lake Michigan declined from 4000/m^2 in 1997 to 918/m^2 in 2007 (David Rockwell, EPA Great Lakes National Program Office (GLNPO), pers. comm.). *Diporeia* experienced a similar pattern at Lake Huron EPA Site 54 (124 m depth) declining from 6000/m^2 in 1999 to 739/m^2 in 2007. Although difficult to collect, live *Diporeia* from Lakes Michigan and Huron represented populations at risk and were ideal for this study.

I did not experience problems collecting live *Diporeia* from stable and abundant populations in both Lake Superior and Cayuga Lake. *Diporeia* density in Lake Superior has been stable while populations in other Great Lakes have declined (Scharold et al. 2004, Auer et al. 2009). Dreissenid mussels have not successfully expanded outside of shallow harbors in Lake Superior, probably due to low levels of dissolved calcium (Grigorovich et al. 2003, 2008). The absence of dreissenid mussels in my Lake Superior study sites is consistent with abundant and healthy populations of *Diporeia*- *Diporeia* at Site 23 B (65 m) oscillated between 1000 and 2000/m^2 between 1999 and 2007, and in 2007, the population density of *Diporeia* at EPA Mid-Continent Ecology Division (MED) Site 53 (39 m) was 3993/m^2 with no dreissenid mussels present (David Rockwell, EPA GLNPO, pers. comm.).

Cayuga Lake is one of the few sites in North America where *Diporeia* populations have not decreased in the presence of dreissenid mussels (Dermott et al. 2005b, Chapter 2). *Diporeia* in Cayuga Lake have persisted throughout this study at levels near 5000/m^2 despite living in direct contact with high levels of quagga mussels.

Exposure Experiments

Diporeia were maintained in a cold room at 5°C temperature and darkness simulating lake-bottom conditions. Microcosms consisted of 250 mL dechlorinated tap water with a substrate consisting of either natural mud or combusted sand or water only. *Diporeia* additions of 5 or 10 individuals per microcosm represented a low population density of 1000 or 2000/m^2 respectively. These exposure experiments included quagga mussel exposure treatments and no mussel controls and were conducted over time periods ranging from 14 to 65 days. *Diporeia* are adapted to sporadic food supplies by having large lipid stores that enable them to withstand long periods without food (Gauvin et. al. 1989). Therefore, competition for food is unlikely to be an important factor in these short-term experiments. Live quagga mussels were collected close in time to the start of each experiment to ensure that their microbial community had not changed from that in the field.

Indirect Exposure- Test of Hypothesis 1

Diporeia were first exposed to water taken from tanks holding quagga mussels, rather than the mussels themselves, as a test of whether the mussels can have indirect effects. Survival rates of three *Diporeia* populations were compared in this experiment including *Diporeia* from Lakes Michigan (EPA Site 40, 170 m depth), Lake Superior (EPA Site 23B, Whitefish Bay at 62 m) and Cayuga Lake (Myers Point at 60 m). After an initial acclimatization period, water within the microcosms was replaced from four-liter tanks containing ten live quagga mussels from different lakes. Three sources of quagga mussels were compared including Lakes Ontario (EPA Site 63, 86 m), Lake Michigan (EPA Site 52B, 54 m), and Cayuga Lake (Myers Point, 60 m depth).

The Lake Superior and Lake Michigan *Diporeia* trials were conducted over a 68-day period starting November 1, 2007. The Cayuga Lake *Diporeia* trial was conducted over a 53-day period starting November 15, 2007. Water from quagga mussel tanks was added to microcosms with *Diporeia* on November 27 and December 5. Healthy *Diporeia* burrow in sediments and dead individuals were removed from the sediment surface during the course of the experiment. *Diporeia* were counted on December 6, 2007 by gently stirring up the sediments and removing swimming individuals. At the end of the experiment on January 4, 2008, a final count was taken for all the *Diporeia* extracted from the sediment. The first count appeared incomplete for the Cayuga Lake trial because it yielded lower numbers than the final count. Subsequent counts indicated that many of the amphipods did not leave the sediment despite stirring. *Diporeia* in the Lake Superior and Lake Michigan trials did not behave similarly to those from Cayuga Lake. Therefore, I have a valid 36 and 65-day count for the Lake Superior and Lake Michigan trials but only a single 50-day count for the Cayuga Lake trial.

Direct Exposure- Tests of Hypotheses 2, 3 and 4

As a test for Hypothesis 2, I evaluated the effects of directly exposing *Diporeia* to increasing levels of quagga mussels. Initially I added five or ten quagga mussels (1000 and 2000/m^2) from either Cayuga Lake or Lake Michigan to microcosms with ten *Diporeia* (2000/m^2) from Cayuga Lake for a two-week period (June 4-June 18, 2008). In summer 2009, I evaluated the effects of quagga mussel densities of 5000 and 10,000/m^2. For such high densities I used larger microcosms (1 liter rather than 250 mL). The experiment ran for 28 days, and each treatment had three replicates with 10 adult *Diporeia*. The *Diporeia* and quagga mussels were collected only from Cayuga Lake for the second experiment.

As a test for Hypothesis 3 and 4, I conducted several exposure experiments using microcosms with 10 adult *Diporeia* as a control and 10 adult *Diporeia* and 10 quagga mussels for treatments. I used a 28-day exposure period and evaluated several combinations of source populations for the two species (Figure 3.1).

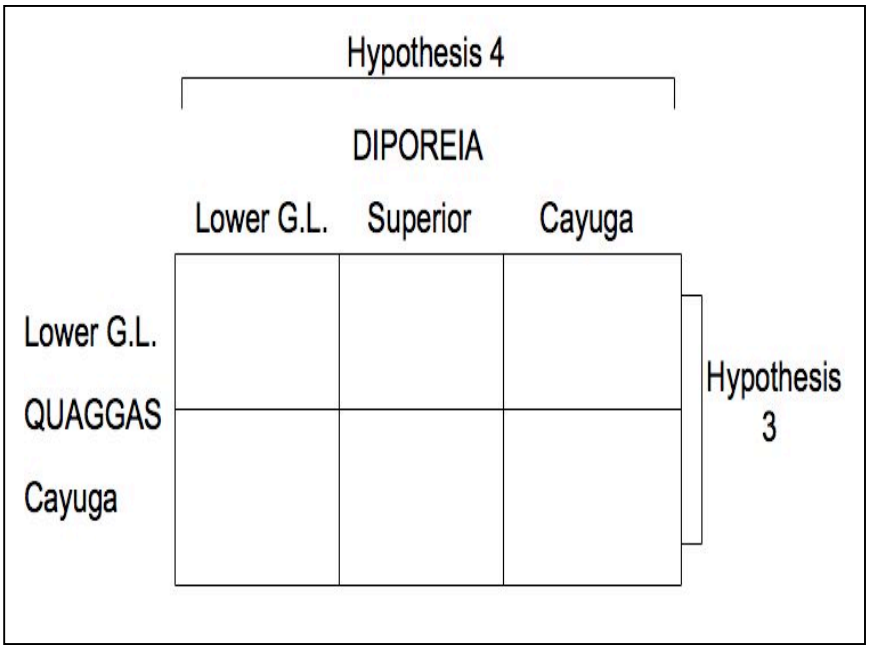

Figure 3.1. Schematic of *Diporeia*/Quagga mussel combinations used in experimental trials. Hypothesis 3 test differences in mortality caused by exposure to quagga mussels from different sources, while Hypothesis 4 test differences in the resiliency of *Diporeia* populations to quagga mussels exposure. "Lower G.L." refers to populations from lakes Michigan, Huron, and Ontario where natural populations of *Diporeia* have declined.

Diporeia from Cayuga Lake were exposed to Lake Michigan quaggas for 28 days starting July 3, 2008. The exposure treatment and no-mussel control had six replicates. *Diporeia* from Lake Huron (EPA Site 54, 124 m depth) were collected on April 19, 2008 and were used to represent a "Lower Great Lakes" population in the above schematic. I directly exposed the *Diporeia* to quagga mussels from Cayuga

Lake and Lake Michigan for 28 days beginning July 16, 2008. *Diporeia* from western Lake Superior (EPA MED Site 053, 39 m) were collected in September, 2008. These *Diporeia* were exposed to quagga mussels from Lake Michigan and Cayuga Lake in the laboratory on November 4, 2008. The two direct exposure treatments and no-mussel control had seven replicates.

Statistical Analysis

The average survival of *Diporeia* in quagga mussel exposure treatments were compared to the survival for the same population in a no mussel control using a student's t-test or a one-way analysis-of-variance (ANOVA) using the software JMP 7.0 (SAS Institute, 2007). Two-tailed p-values less than 0.10 indicated significant differences between group means. In cases of comparing the control to two or more treatments, a Tukey's honestly significant difference (HSD) test was used for confirmation if the initial ANOVA indicated that there was a probability for a significant difference.

RESULTS

Indirect exposure- test of Hypothesis 1

Diporeia from Lake Michigan (Station 40) had the lowest survival rates in my experiment, averaging only 35.7% (s.e. 3.8%) survival over 36 days and 13.0% over 65 days (Figure 3.2). These results are from no mussel controls- due to the poor survival, we did not expose this population to water from tanks containing quagga mussels. Averaged over all treatments, *Diporeia* from Lake Superior had a survival of 80.5% (s.e. 3.2%) over the 36-day period and 35.0% (s.e. 4.1%) over the 65-day

period. *Diporeia* from Cayuga Lake had an average survival of 75.0% (s.e. 4.4%) over the 50-day period.

As previously described, the *Diporeia* were exposed to water from quagga mussel tanks and not directly to mussels. The average survival for the Lake Superior *Diporeia* population after 36 days was 86% (s.e. 5.2%) for the control, relative to 86%

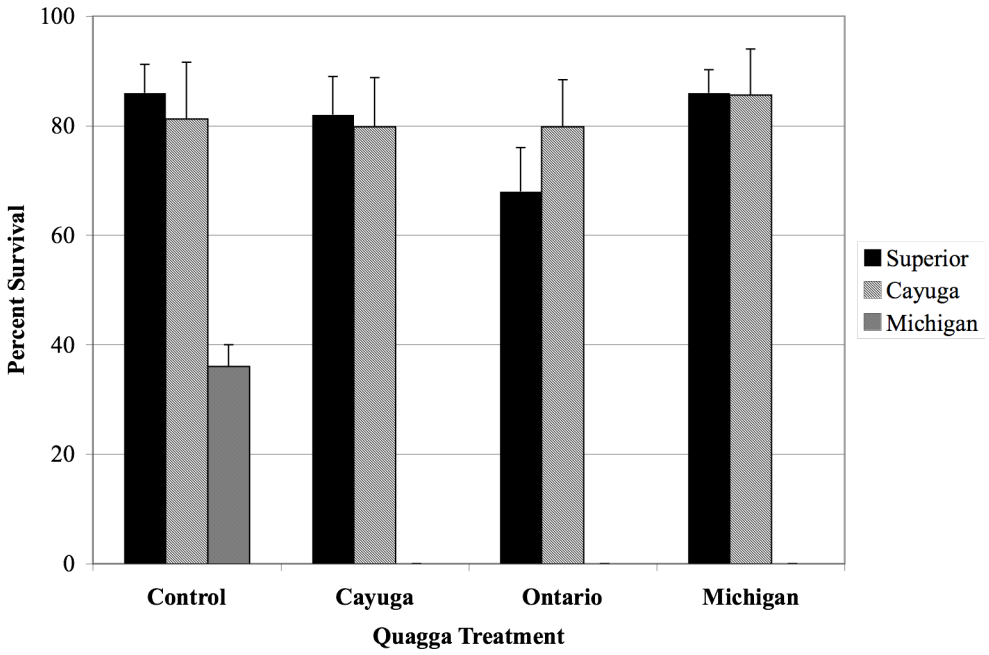

Figure 3.2. Survival rates over 36 days for three *Diporeia* populations (Superior, Cayuga, Michigan see color bar in legend) during indirect exposure to three different quagga mussel populations and a no mussel control. Indirect exposure refers to no direct contact with mussels, but rather to water and excretion products taken from mussel tanks.

(s.e. 4.2%) exposed to Lake Michigan quaggas, 68% (s.e. 8.0%) exposed to Lake Ontario quaggas, and 82% (s.e. 7.0%) exposed to Cayuga Lake quaggas (Figure 3.2). Although survival for the Lake Ontario quagga treatment was lowest, the average survival rates for the control and three survival treatments were not significantly

different (ANOVA, p=0.16). The average survival for Cayuga Lake *Diporeia* after 50 days was 74% (s.e.10.4%) for the control, relative to 80% (s.e. 8.4%) exposed to Lake Michigan quaggas, 72% (s.e. 8.6%) exposed to Lake Ontario quaggas, and 72% (s.e. 9.0%) exposed to Cayuga Lake quaggas (not significantly different, ANOVA, p=0.91). Therefore, for *Diporeia* of both Lake Superior and Cayuga Lake, there were no significant differences in survival between the no mussel control and the indirect mussel exposure treatments using water from tanks for quagga mussels from Lake Michigan, Lake Ontario, and Cayuga Lake.

Direct Exposure- Tests of Hypotheses 2, 3 and 4

I evaluated the effects of increasing levels of quagga mussel abundance as a test of Hypothesis 2. Survival of Cayuga *Diporeia* after direct exposure to Cayuga quagga mussels at densities of 1000 and 2000/m^2 were slightly higher but not significantly different (80% for both, s.e. 4.5 and 3.2%) than for the no-mussel controls (77%, s.e. 3.2%, ANOVA, p=0.75). Exposing Cayuga *Diporeia* to quagga mussels from Lake Michigan yielded similar results. In a later experiment, with quagga mussel densities elevated to 5000 and 10000/m^2, there was again no significant difference between the two treatments and the no-mussel control over 28 days (ANOVA, p=0.37). The 5000/m^2 treatment had highest survival (97%, s.e. 3.3%), followed by the 10,000/m^2 treatment (93%, s.e. 3.3%) and the no mussel control (87%, s.e. 6.7%)

Tests of Hypothesis 3 and 4 compared different combinations of *Diporeia* and quagga mussel source populations, both organisms at 2000/m^2 levels and conducted over 28 days. For Cayuga Lake *Diporeia,* survival was slightly higher in the no-mussel control (80%, s.e. 3.7%) than when exposed to mussels from Lake Michigan (74%, s.e. 6.9%) but the difference was not significant (Student's t-test, p=0.50) (Table

3.2). Survival of Lake Huron *Diporeia* was also higher for the no mussel control (70%, s.e. 4.5%) but not significantly different from treatments using quagga mussels from Cayuga Lake or Lake Michigan (both were 60%, s.e. 10%) (ANOVA, p=0.76). For Lake Superior *Diporeia* there were again no significant differences between the control and two mussel treatments (ANOVA, p=0.84), the average survival for

Table 3.2. Percent survival (s.e.) for *Diporeia* 28-Day Direct Exposure Experiments

			Quagga mussel source		($p<0.10$)
Source	Date	Control	Michigan	Cayuga	significant?
Huron	7/16/08	70(4.5)	60(10)	60(10)	no, p= 0.76
Superior	11/4/08	76(4.2)	77(6.5)	80(5.8)	no, p= 0.84
Cayuga	7/3/08	80(3.7)	74(6.9)		no, p= 0.50
Cayuga	6/10/09	90(4.5)		96(2.4)	no, p= 0.38

Cayuga Lake mussel exposures was 80%, 77% for Lake Michigan mussel exposures, and 76% for the no-mussel control. These findings suggest that direct exposure of *Diporeia* to quagga mussels from three different lakes has no significant effect on survival.

DISCUSSION

My exposure experiments included *Diporeia* populations from lakes experiencing major declines as well as lakes with healthy populations. First, I found that indirect exposure to quagga mussels (via water) had no significant effect on survival of *Diporeia* relative to no-mussel controls. This suggests that the advection of digestion products from shallow mussel beds is an unlikely mechanism for deep *Diporeia* population declines observed in affected lakes. Secondly, I found that

Diporeia can tolerate direct exposure to quagga mussels at densities as high as 10,000/m^2 with no discernable effect on survival. Lastly, the source of quagga mussels made no significant difference in *Diporeia* survival in these experiments. These findings lead me to reject my initial hypothesis that short-term exposure to quagga mussels or their digestion products is lethal to *Diporeia*.

These findings are consistent with those of Faisal (2008). The Faisal study included a continuation of Messick et al. (2004)'s approach by surveying parasites and disease in *Diporeia* populations from all of the Great Lakes during EPA shipboard surveys in summer 2007 and 2008. *Diporeia* were collected for traditional histological analysis of pathogens and parasites (preserved in formalin), virology (frozen), as well as for identification of the microbial community using Terminal-restriction fragment length polymorphism (T-RFLP).

Faisal's pathogen survey provided little explanation for the observed *Diporeia* declines. *Diporeia* from affected and unaffected lakes appeared healthy, with no abnormalities or signs of disease (Faisal 2008). Larval stages of acanthocephalan, cestode, and nematode parasites were commonly found, but not to the extent of being lethal. For example, *Diporeia* collected from Lake Huron in 2007 were nearly all infected by parasites, particularly acanthocephalans. *Diporeia* from each lake harbored slightly different bacterial communities. For instance, *Diporeia* from Lake Michigan were found to have a more diverse bacterial community than that of *Diporeia* from Lake Superior. Known bacterial pathogens such as *Flavobacterium* were present in most populations, and ß-proteobacteria were more common in *Diporeia* from Lake Michigan. *Diporeia* from Lake Michigan and Lake Huron were confirmed (using polymerase chain reaction (PCR)) to be carrying Viral Hemorrhagic Septicemia (VHS) during different times in the survey. Although implicated as the cause of several fish kills in the Great Lakes, the virus has unknown effects on

invertebrate carriers. Although finding many interesting differences, Faisal (2008) did not find a clear pathogen based explanation for declines in *Diporeia* populations of Lakes Huron, Michigan, and Ontario.

Dr. Faisal's findings confirm that the *Diporeia* source populations used in my experiments were generally healthy although having variable parasite loads and microbial communities. The survival of these *Diporeia* populations in my experiments was not significantly affected by exposure to quagga mussels from lakes Michigan, Ontario, and Cayuga. I therefore conclude that quagga mussels have not contributed to the decline of *Diporeia* in several of the Great Lakes by acting as a vector for pathogens deadly to the native amphipod. It is difficult to say whether a pathogen not associated with dreissenid mussels could have caused the rapid disappearance of *Diporeia* in the Great Lakes because of the low infection rates measured in pathogen surveys. If dreissenids are involved in the decline of *Diporeia*, it is more likely due to competition for food.

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CHAPTER 4: EVALUATING FOOD LIMITATION OF *DIPOREIA* BY QUAGGA MUSSELS IN THE LABORATORY

ABSTRACT

One hypothesis for the disappearance of the benthic amphipod *Diporeia* from many of the Great Lakes is competition for food by exotic dreissenid mussels. In this chapter I investigate the effects of direct interaction of quagga mussels on *Diporeia* condition and survival over a three-month period with mussel densities of 0, 700, and 3500/m^2. Contrary to my expectations, *Diporeia* exposed to quagga mussels weighed more than *Diporeia* in no-mussel controls at the end of the three-month period. Survival rates and fatty acid composition were not significantly different. Substrate preference experiments indicate that *Diporeia* prefers substrates with live quagga mussels over substrates without mussels or with structural substitutes (empty shells or crucibles). These two findings indicate that *Diporeia* benefits from direct interaction with quagga mussels. If quagga mussels are responsible for the decline of *Diporeia*, it is likely due to the remote effects of shallow mussel beds intercepting food for deep *Diporeia* populations. This scenario is consistent with field surveys in the Great Lakes.

INTRODUCTION

Food limitation by dreissenid mussels is one hypothesis for the decline of *Diporeia* in many of the Great Lakes (Chapter 1). Field surveys in the Great Lakes indicate that *Diporeia* populations declined prior to direct contact with quagga mussels, indicating that shallow mussel beds remotely affect deeper *Diporeia*. Although examples of coexistence are rare, *Diporeia* populations in the Finger Lakes of central New York persist despite living in direct contact with dreissenid mussels

(Chapter 2). Therefore, it is unclear whether direct contact with dreissenids has a positive or negative effect on *Diporeia*. Short-term (28-day) exposure experiments showed no evidence that mussels are toxic or transmit pathogens to *Diporeia* (Chapter 3). This chapter describes results of experiments of longer duration (three months) where food limitation is more likely to be a factor.

Diporeia was initially thought to be an indiscriminate deposit feeder, ingesting organic matter and bacteria within sediments (Marzolf 1965). The importance of seasonal diatom blooms became clear during monthly sampling of a *Diporeia* population at a site at 29 m depth in Lake Michigan in 1984 (Gardner et al. 1985). The average lipid content of *Diporeia* increased from 26% to 50% between April and June, a period of high flux to sediments of biogenic silica (a tracer of diatoms) and associated lipids as measured in traps (Gardner et al. 1989). *Diporeia* were estimated to assimilate up to 61% of the algal carbon deposited after a bloom event in Lake Michigan, making them an important link of benthic and pelagic ecosystems (Fitzgerald and Gardner 1993). Diatoms are a high quality food relative to other algal groups and are an excellent source of lipids, particularly several polyunsaturated fatty acids (PUFAs) that cannot be synthesized directly by animals (Brett and Muller-Navarra 1997). The large cell size of diatoms also promotes rapid sinking to the lake floor, so that the organic matter is relatively fresh with little decomposition or grazing.

Diporeia accumulate vast lipid stores that help them withstand seasonal cycles of feast and famine in cold deep lakes. In the field, lipid content of Lake Michigan *Diporeia* decreases gradually from July to September, suggesting that lipid stores are utilized during periods of low flux (Gardner et al. 1985). In laboratory measurements, *Diporeia* lipid content decreased from 30% at the time of collection to 12% after 120 days of fasting (Gauvin et al. 1989). Individuals lived in water without food or substrate for as long as 217 days. This long-term survival was attributed to the

amphipod's low metabolism at low water temperatures, reflected by low excretion rates for ammonium and phosphorus. Lipids are not just important for energy storage-PUFAs in particular are known for enhancing growth and reproduction (Brett and Navarra 1997). PUFAs stay fluid at low temperatures, making them essential for membranes of coldwater organisms.

Lipid content in *Diporeia* is an indicator of individual condition as well as the overall capacity of a lake ecosystem to support the population. A lipid content of 20% has been offered as the minimum required for successful reproduction of the similar species *Monoporeia affinis* of Europe (Hill et al. 1992). Lipid content of *M. affinis* in Sweden's oligotrophic Lake Vättern declined to 10% in 2001, leading to low fecundity and a high percentage of dead broods (Sundelin et al. 2008). Reproduction improved the following year when food fluxes were higher and lipid content increased to 20%. Historical measurements of *Diporeia* lipid content in lakes Superior (Auer et al. 2009), Huron (Guiguer and Barton 2002), Michigan, and Ontario (Caveletto et al. 1996) vary from 25 to 35%, all above the proposed minimum.

My measurements of lipid content for *Diporeia* collected in Cayuga Lake in June, 2008 at 40 m depth averaged 14.9% (s.e. 3.3%)(Chapter 2), lower than the 33.1% lipid content measured from *Diporeia* in this lake in June, 1964 (Green 1971). During this 50-year time period, lake productivity had declined slightly and dreissenids were established. *Diporeia* collected from Owasco Lake in June, 2008 had a much higher lipid content of 51.6% (s.e. 3.1%)(Chapter 2). The two lakes are similar in trophic state but Cayuga Lake has deep dwelling quagga mussels while Owasco Lake only has shallow zebra mussels. Cayuga *Diporeia* had lower levels of the diatom tracer palmitoleic acid (16:1w7) than those of Owasco Lake, but a higher proportion of the important PUFAs eicosapentaenoic acid (EPA) and arachidonic acid

(ARA). This data suggests that diet and the presence of dreissenids can influence the overall lipid content of *Diporeia* as well as the specific fatty acid composition.

In this chapter, I evaluate the influence of diet and dreissenid competition on the condition and fatty acid composition of *Diporeia*. I present data from a three-month experiment offering *Diporeia* from Cayuga Lake different foods. One feeding treatment added leaf debris commonly found in the substrate of Cayuga Lake that has been hypothesized to help *Diporeia* persist in the presence of dreissenid mussels (Dermott et al. 2005). A second three-month experiment investigated the effects of two different levels of quagga mussels. My hypothesis was that the presence of quagga mussels would have a negative impact on amphipod condition because the mussels would intercept food and deposit lower quality digestion products (pseudofeces). I also present data from substrate preference experiments that evaluate *Diporeia*'s behavioral response to the presence of quagga mussels.

MATERIALS AND METHODS

In the first experiment, *Diporeia* collected from Cayuga Lake were kept in 2L plastic containers of dechlorinated tap water (Lake Ontario source) and offered different potential food items beginning August 4, 2009. Groups of 15 *Diporeia* were added to each microcosm for a density of 525/m^2. The food items included screened (500 μm) mud, additions of a liquid algal suspension supplement (Phyto-Gold), coarse leaf litter separated from sediments, and quagga mussels. Water was changed weekly. The experiment ended November 2, 2009 when survival was assessed. Individual *Diporeia* were flash frozen for later fatty acid analysis.

In the second experiment, groups of 20 *Diporeia* (700/m^2 abundance) collected from Cayuga Lake were added to microcosms with screened (500 μm) substrate on

Table 4.1 Design of 90-day feeding and exposure experiments

Trial 1 (8/4/09-11/2/09)

15 adult *Diporeia* from Cayuga Lake (collected 6/16/09 at 40 m) per 2 L microcosm with bottom area 0.0286 m^2

Treatments (no replicates)

1)"fasting" (water only)
2) mud substrate
3) quagga mussels (no substrate)
4) algal liquid suspension added (no substrate)
5) terrestrial organic matter added (no substrate)

Trial 2 (12/2/09-3/3/10)

20 adult *Diporeia* from Cayuga Lake (collected 11/20/09 at 40 m) per 2 L microcosm with bottom area 0.0286 m^2

Treatments (5 replicates each)

Control (mud substrate, no mussels)
"Low Q" (mud substrate, 20 live quagga mussels added (simulating 700/m^2 density)
"High H" (mud substrate, 100 live quagga mussels added (simulating 3500/m^2 density)

November 20, 2009. Two levels of quagga mussel abundance were defined as "low" (20 added for a density of 700/m^2) and "high" (100 added for a density of 3500/m^2) as well as a no-mussel control. Each treatment had five replicates. Water was completely replaced in the containers every week resuspending the sediment. The experiment ended on March 3, 2010 and all survivors were counted, measured for length (mm), and flash frozen for later fatty acid analysis.

I measured the fatty acid composition of the individual *Diporeia* in the laboratory of Dr. Mark Teece at SUNY-ESF. The five largest individuals without broods from each treatment were selected. Frozen specimens were freeze-dried and weighed. A 2:1 mixture of chloroform and methanol was used for the extraction of fatty acids. Gas chromatography (Shimadzu GC 17-A) separated and measured the mass of specific fatty acids relative to an internal C23 lipid standard. The data is presented here as percent of total lipids that each fatty acid represents.

I conducted a series of substrate preference experiments to investigate the behavioral response of *Diporeia* to quagga mussels (Table 4.2). These were conducted in 10-gallon aquaria filled with dechlorinated tap water kept at 5°C in a cold room. Each substrate was represented by five replicate petri dishes. Each dish was covered with a coarse mesh to keep quagga mussels in but allow amphipods to enter and leave. Amphipods were added at the surface and given a time period to select a substrate. At the end of each experiment the petri dishes were covered and removed. Sediment was sieved and *Diporeia* within each dish was counted.

The first substrate preference experiment ran from July 10-15, 2009. Three substrates to choose from included mud from Cayuga Lake, mud with 10 live quagga mussels, and mud with 10 empty mussel shells. 100 amphipods from Cayuga Lake were released into the tank and given 96 hours to choose substrate. A second experiment replaced the empty shells with ceramic crucibles about 1 cm in diameter.

Table 4.2. Substrate preference experiments

Trial	Date	Replicates	Substrate options
Live mussels and empty shells			100 *Diporeia* added to tank
1	July 10-15, 2009	5	1) mud alone
		5	2) mud and ten live quagga mussels
		5	3) mud and ten empty quagga shells
Live mussels and artificial shelter (crucibles)			80 *Diporeia* added to tank
2	July 10-15, 2009	5	1) mud alone
		5	2) mud and ten live quagga mussels
		5	3) mud and ten ceramic crucibles
Varying density of live quagga mussels			100 *Diporeia* added to tank
3	July, 2010	8	1) mud alone
		3	2) mud and five small quagga mussels
		3	3) mud and ten small quagga mussels
		5	4) mud and five large quagga mussels
		5	5) mud and ten large quagga mussels

* five quagga mussels per dish represents 1770/m^2, ten mussels represent 3540/m^2

The experiment was run from July 10-15, 2009. 80 amphipods were released into the tank and allowed 96 hours to choose substrate. A third experiment examined how the density of mussels affected the substrate selection by the amphipods. Substrates with "low" (five, 1770/m^2) and "high" (10, 3540/m^2) abundances of either small or large mussels were compared to the no-mussel controls. The control had eight replicates while the substrates with small mussels had three replicates each and the two substrates with large mussels had five replicates each. 100 amphipods were released in the tank and allowed 96 hours to choose substrate. Due to a variable number of replicates for treatments, the results were weighted using the proportion of the total number of dishes (24) represented by each substrate.

Survival rate and substrate selection data was analyzed using a one-way analysis-of-variance (ANOVA) using the software JMP 7.0 (SAS Institute, 2007). P-values less than 0.10 indicated significant differences between group means. Tukey's honestly significant difference (HSD) test was used for confirmation if the initial ANOVA indicated that there was a probability for a significant difference.

RESULTS

Feeding Experiments

For the initial three-month experiment, the highest survival rates were for the *Diporeia* in mud alone (80%) or with quagga mussels alone (73%) (Table 4.3). The lowest survival was for *Diporeia* in water alone with no added food (27%). Treatments with leaf litter or weekly additions of algal supplement and no substrate had survival rates of 40%. Although survival for the mud treatment was twice that of the leaf litter treatment, the surviving adult *Diporeia* in the leaf litter treatment were larger (7.56 mm (s.e. 0.19 mm, n=4) relative to the mud treatment (6.45 mm (s.e. 0.26,n=4)) and weighed more (1.36 mg (s.e. 0.18) compared to 0.64 mg (s.e. 0.08) at the end of the three-month period.

The second three-month experiment had five replicates for each quagga mussel treatment and the no-mussel control. Survival rates for the no-mussel control (59%, s.e. 9.3%) were lower than the previous experiment and not significantly different from the survival rates in the "low" (62%, s.e. 4.1%) and "high"(43%, s.e. 8.2%) quagga mussel treatments (Table 4.3, ANOVA p=0.20).

Although survival was lowest for the "high" quagga mussel treatment, the average length (mm) of surviving *Diporeia* was larger (Figure 4.2). Average length of *Diporeia* in the three treatments was significantly different, increasing from 5.88 mm

(s.e. 0.14 mm, n=59) for the no-mussel control to 6.44 mm (s.e. 0.15 mm, n=63) for *Diporeia* exposed to "low" levels of quagga mussels to 6.75 mm (s.e. 0.17 mm, n=43) for *Diporeia* exposed to "high" levels of quagga mussels (Figure 4.1, ANOVA, $p<0.05$). Average weight of a 6-7 mm adult *Diporeia* was also significantly lower in the control (0.54 mg, s.e. 0.06 mg, n=4) than for the "low quagga" treatment (0.79 mg, s.e. 0.06 mg, n=4) and the "high quagga" treatment (0.74 mg, s.e. 0.04 mg, n=4) (ANOVA, $p<0.05$). There were also more gravid females per microcosm (2.0, s.e. 0.45) for the low and high quagga treatments than in the no mussel control (1.2, s.e. 0.37), but this difference was not significant (ANOVA, p=0.34).

Table 4.3 Results of three-month feeding and exposure experiments.

Experiment 1 (8/4/09-11/2/09)

Treatment	% Survival of 15 *Diporeia*
Fasting (water only)	27%
Mud alone	80%
Quagga mussels alone	75%
Leaf litter alone	40%
Algal supplement alone	40%

Experiment 2 (12/2/09-3/3/10)

Survival and Fecundity

Treatment	replicates	survival(%)	%gravid
Control	5	59 (9.3)	6.0 (1.8)
Low	5	62 (4.1)	10 (2.2)
High	5	43 (8.2)	10 (2.2)

Average Length and Weight

Treatment	n	length (mm)	n	weight (mg)
Control	59	5.88 (0.14)	4	0.54 (0.06)
Low	63	6.44 (0.15)	4	0.79 (0.06)
High	43	6.75 (0.17)	4	0.74 (0.04)

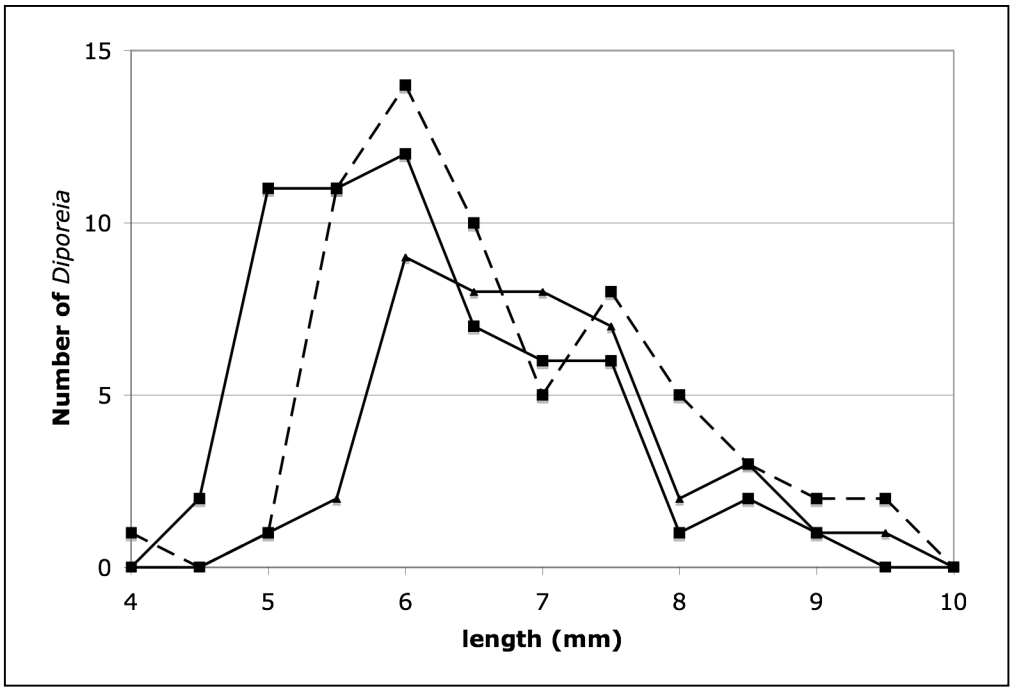

Figure 4.1. Size distribution of survivors for control (solid line with squares), low levels of quagga mussels (dashed line with squares) and high levels of quagga mussels (solid line with triangles).

Fatty acid content

The fatty acid signature for Cayuga *Diporeia* after three months in the laboratory was similar to that of organisms collected in the field (Table 4.4). All laboratory organisms had a higher proportion of the monounsaturated fatty acid (MUFA) oleic acid (18:1w9) and a lower proportion of the bacterial tracer MUFA vaccenic acid (18:1w7) relative to *Diporeia* measured soon after field collection. *Diporeia* from the no-mussel control also showed a higher proportion of the MUFA 16:1w9 and a lower proportion of the diatom tracer (Goedkoop et al. 2000) palmitoleic acid (16:1w7). *Diporeia* in the leaf litter treatment had a higher proportion of the saturated fatty acid palmitic acid (16:0) and the diatom tracer palmitoleic acid (16:1w7) and a lower proportion of polyunsaturated fatty acids (PUFAs), particularly DHA (22:6w3). Terrestrial indicators 18:2w6 and 18:3w3 were similar in all treatments including the one that included terrestrial leaf litter.

There were analytical problems in using the C23 internal standard for the determination of absolute lipid content of some individual *Diporeia*. The successful runs measured lipid content of adult non-gravid *Diporeia* from the no-mussel control (n=1) as 31.7% lipid per dry weight while *Diporeia* in the "high" mussel treatment were 37.9% lipid (s.e. 10.4%, n=3). *Diporeia* from the "leaf litter" treatment were 54.8% lipid (s.e. 8.1%, n=3).

Substrate Preference Experiments

In all of the substrate choice experiments comparing substrates with live quagga mussels with substrates with no mussels, a preference for substrate with live mussels was found (Table 4.5). For the first experiment, the percentage of amphipods selecting substrate with live quaggas and fine sediment was 67% (s.e. 11%),

Table 4.4 Average proportion (% of total lipid content) of specific fatty acids for individual *Diporeia* from Cayuga Lake before (field) and after three-month experiments. Treatments include "Control"(mud substrate only), "High Q" (mud substrate and ten live quagga mussels simulating density of 3540/m^2), "Quagga" (live quagga mussels only, no substrate), and "Organic" (terrestrial organic matter, no substrate). Specific fatty acids are organized and summed by group. Average length (mm) and weight (mg) included at bottom of table.

	Field		**Control**	**High Q**		**Quagga**	**Organic**	
	n=8		**n=1**	**n=3**		**n=1**	**n=3**	
	average	s.e.		avg	s.e.	only	avg	s.e.
Saturated (SAFA):								
14:0	0.3	0.2	0.0	0.0	0.0	0.0	0.0	0.0
'16:0	14.6	1.9	13.4	14.1	2.0	16.0	21.2	1.1
'18:0	3.9	0.6	4.3	3.7	0.9	4.3	1.9	0.2
Sum	**18.7**	**2.0**	**17.7**	**17.8**	**1.2**	**20.3**	**23.1**	1.0
Monounsaturated (MUFA):								
14:1	0.1	0.1	0.0	0.2	0.1	0.0	1.0	0.4
'16:1w7	7.8	1.9	1.2	4.0	1.7	7.1	11.2	0.9
'16:1w9	0.7	0.3	9.1	2.8	2.2	0.0	0.7	0.1
18:1w7	11.0	4.4	0.0	2.2	2.2	0.0	6.4	3.5
18:1w9	22.0	4.8	33.0	38.1	3.7	34.8	31.9	4.7
Sum	**41.7**	**1.7**	**43.3**	**47.3**	**3.3**	**41.9**	**51.3**	0.9
Diunsaturated (DUFA):								
18:2w6	6.6	1.0	4.4	3.0	0.7	4.0	3.0	0.2
Sum	**6.6**	**1.0**	**4.4**	**3.0**	**0.7**	**4.0**	**3.0**	0.2
Polyunsaturated (PUFA):								
18:3w3	2.6	0.2	4.1	3.4	1.0	4.4	1.7	0.1
18:4w3	1.6	0.3	1.3	1.4	0.2	1.8	0.8	0.1
20:4w6 ARA	5.0	1.0	6.8	5.7	0.8	3.7	4.1	0.5
20:5w3 EPA	15.6	1.1	16.3	15.4	1.8	16.1	13.0	0.3
22:6w3 DHA	8.1	2.0	6.1	6.0	1.6	7.7	2.9	0.1
Sum	**32.9**	**3.7**	**34.6**	**31.8**	**4.8**	**33.8**	**22.6**	0.7
	n=8		**n=4**	**n=4**		**n=1**	**n=4**	
Dry Weight of *Diporeia* (mg)	**0.65**	**0.07**	**0.54**	**0.75**	**0.07**	**0.96**	**1.36**	**0.18**
			s.e. 0.06					
Length of *Diporeia*(mm)			**6.48**	**6.55**	**0.21**	**7.69**	**7.56**	**0.19**
			s.e. 0.31					

significantly higher (ANOVA, $p<0.05$) than for the no-mussel control (21% (s.e. 9%), $p=0.006$, Tukey's HSD) and for substrate with empty shells (8% (s.e. 4%), $p=0.001$, Tukey's HSD). This pattern remained when empty shells were replaced by porcelain crucibles. The percentage of amphipods selecting substrates with live quaggas and fine sediment was 60% (s.e. 19%), significantly higher (ANOVA, $p<0.05$) than for the control (10% (s.e. 10%), $p=0.03$, Tukey's HSD) and for the crucibles (15% (s.e. 11%),$p=0.05$, Tukey's HSD). For the third experiment, *Diporeia* were most likely to select substrates with ten small mussels (36.8%) or five large mussels (28.8%), followed by ten large mussels (15%) and five small mussels (10.4%) (Table 4.5, Figure 4.2). No *Diporeia* selected the no-mussel control that represented one-third of the available substrate.

Table 4.5 Results of substrate preference experiments. Percent % of total *Diporeia* selecting each substrate with one s.e. The final trial is corrected for proportion of dishes (out of 24) represented by each substrate.

		% of *Diporeia* selecting substrate				
Trial		Control		Mussels		"Shelter"
Live mussels and empty shells		21% (9%)		67% (11%)		9%(4%)
Live mussels and artificial shells (crucibles)		10%(10%)		60% (19%)		15%(11%)
		none	5sm	10sm	5lg	10lg
Varying density of live quagga mussels	#dish	8	3	3	5	5
	avg	0%	10.4%	36.8%	28.8%	15%
	s.e.	(0%)	(4%)	(33.6%)	(13.9%)	(5.3%)

DISCUSSION

At the end of my three-month experiments, *Diporeia* survival was high (60-80%) when offered a natural mud substrate and not significantly different (ANOVA, $p<0.05$) from treatments with living quagga mussels with and without substrate. Survival was lowest for *Diporeia* in water alone (27%) and also low (40%) for amphipods offered an algal suspension or leaf litter. However, adult *Diporeia* in treatments with quagga mussels or leaf litter were on average heavier (0.75 mg and 1.36 mg) than *Diporeia* in mud only controls (0.54 mg) at the end of the experiment, indicating that the addition of these items enhanced growth of *Diporeia*.

Previous feeding studies have also not found a correlation of condition and survival. Kainz et al. (2010) compared *Diporeia* fed three different algal foods (green algae, diatoms, and cyanophytes) to those fasting for 30 days. Fasting *Diporeia* experienced a 28% decline in dry weight and a 60% decline in lipid content, while *Diporeia* fed green algae or diatoms maintained weight and lipid content during the feeding trial. However, survival rates were similar (ranging from 60-70%) for the green algae, diatom, and fasting treatments. No *Diporeia* survived in the cyanophyte-fed treatment. The authors concluded that survival was not related to the quantity and quality of food. Condition measured by nucleic acid ratios RNA/DNA was highest in the diatom-fed treatment, the only diet in the study that contained detectable amounts of the PUFAs DHA and EPA.

My exposure experiments are consistent with field observations of *Diporeia* and *Dreissena* in Lake Michigan. *Diporeia* populations at two sites of 45 m depth in eastern Lake Michigan (H-31 and M-45) were closely tracked as dreissenids became established (Nalepa et al. 2006). Rather than experiencing a decline in condition after coming into contact with dreissenids, there was little change in *Diporeia* length-weight relationships from 1994 to 2001. Mean lipid content of *Diporeia* at H-31 had

declined from 26-32% in the late 1980s (pre-dreissenids) to only 15% in 1994 when dreissenids were still very rare at that depth. However, as *Diporeia* abundance decreased and dreissenid abundance increased, lipid content of the remaining *Diporeia* returned to pre-dreissenid levels near 30%. *Diporeia* in my experiments utilized pseudofeces or epiphyte growth on quagga mussel shells as food and maintained weight and lipid content. Although consistent with *Diporeia* maintaining weight and lipid content in the presence of dreissenids, my experiments do not help to explain the collapse of *Diporeia* populations that occurred at the two Lake Michigan sites in 1997 and 2000. Size frequency data at the two sites suggests that recruitment was generally consistent (except in 1994 at Site H-31, when lipid content was low at 15%), but that the collapse occurred due to the poor survival of young-of-year *Diporeia* to juveniles (Nalepa et al. 2006).

My substrate experiments indicate that *Diporeia* have a clear preference for substrates with live quagga mussels relative to substrates without mussels. Tests with empty shells and porcelain crucibles confirm that this preference does not involve seeking physical shelter but instead *Diporeia* were attracted to something that only live mussels can provide such as increased water circulation or food sources such as periphyton on shells or pseudofeces. These findings are intriguing because it suggests that the amphipods actively sought out what has been considered a harmful competitor. The selection is consistent with my previous findings that *Diporeia* can live for long periods in the presence of quagga mussels and in fact appear to benefit nutritionally from direct contact.

Despite my conclusion that *Diporeia* can benefit from direct contact with quagga mussels, it is likely that the remote effects of shallow mussel beds has reduced the food supply for profundal *Diporeia* populations. The extent of the spring phytoplankton bloom has dramatically decreased in the past decade in Lake Michigan

(Fahenstiel et al. 2010) and Lake Huron (Barbiero et al. 2011). For the isothermal mixed layer of Lake Michigan in springtime, chl *a* and phytoplankton biomass has declined 66% and 87% respectively from 1995-98 levels to 2007-2008. A similar decline in the extent of spring blooms in 2002-2003 has been detected using satellite imagery of Lake Huron (Barbiero et al. 2011). The disappearance of the spring bloom in Lake Michigan is consistent with the increased filtering capacity of the rapidly expanding slope populations of quagga mussels from 30-90 m depth (Vanderploeg et al. 2010). In Lake Huron, a decrease in nutrient levels may be a more likely driver because dreissenids are much less established (Barbiero et al. 2011). Either way, the recent disappearance of the spring bloom considerably reduces the availability of high value diatom food to the lake bottom and is an obstacle to the restoration of *Diporeia* populations in the Great Lakes.

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